THE UNIVERSITY OF ALBERTA

"The morphology and functions of the reproductive systems of the mountain pine beetle, Dendroctonus monticolae Hopk. (Coleoptera : Scolytidae)"

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR

THE DEGREE OF MASTER OF SCIENCE

DEPARTMENT OR DIVISION ENTOMOLOGY

by

Herbert Frederick Cerezke

EDMONTON, ALBERTA

THE MORPHOLOGY AND FUNCTIONS OF THE REPRODUCTIVE SYSTEMS OF THE MOUNTAIN PINE BEETLE, *DENDROCTONUS MONTICOLAE* HOPK. (COLEOPTERA : SCOLYTIDAE)

by

H. F. CEREZKE

TABLE OF CONTENTS

ABSTRACT

The reproductive systems of the male and female mountain pine beetle, Dendroctonus monticolae Hopkins are described and illustrated, and some morphological changes during the adult life cycle are noted. Descriptions are also given for the associated musculature of the male genital apparatus. Some interpretation has been given to the functions of the reproductive components, on the basis of studies of their activity during the processes of mating, sperm transfer, egg formation, and ovulation. Finally, the reproductive systems are briefly discussed from the viewpoints of evolution and fecundity.

ACKNOWLEDGEMENTS

I am indebted to my supervisor Professor B. Hocking, Head of the Department of Entomology, University of Alberta, for his invaluable guidance, criticisms, and suggestions for the preparation of this manuscript. Appreciation is expressed to Drs. J. Sharplin, G.E. Ball, and W.G. Evans, also of the Department of Entomology, for their encouragement and help on techniques. I am also grateful to Drs. A.B. Ewen and M. Shamsuddin, former graduate students of the Department of Entomology, who provided many hints on histological technique.

Initiation of this study was particularly encouraged by the following members of the Forest Entomology and Pathology Laboratory, Calgary, Alberta: Mr. G.R. Hopping, former Officer-in-Charge of the Calgary Laboratory, and Drs. R.W. Reid and R.F. Shepherd. I express my sincere thanks to them for their enlightening discussions and suggestions and for reviewing the manuscript. Dr. Shepherd, as Research Advisor, has assisted in many other ways during the thesis preparation. His help and advice is greatly appreciated.

During the course of this study many collections of *Dendroctonus* species were received from the Forest Insect Survey Personnel of the Forest Entomology laboratories at Vernon and Victoria, British Columbia and from Juneau, Alaska. I extend thanks to all collectors concerned for their co-operation.

Permission to use these Department data for thesis purposes has been granted by Dr. M.L. Prebble, Director of the Forest Entomology and Pathology Branch, Ottawa. Appreciation is expressed to Dr. Prebble and to Dr. B.M. McGugan, Associate Director of the Forest Entomology and Pathology Branch, who reviewed the manuscript.

Resolution 5: The Naval Postgraduate School, the Joint Chiefs of Staff and the Defense Department should be urged to provide more and better training in [illegible] . . . research. [illegible] of the Joint Strategic and Tactical Planning [illegible]. [illegible] appreciation in [illegible] to [illegible] and so on. [illegible] Resolution Twelve: If the Joint Strategic and Tactical Planning System, was to achieve its potential.

LIST OF CHARTS, PLATES, AND FIGURES

INTRODUCTION

This paper deals with the male and female organs of reproduction of the mountain pine beetle, Dendroctonus monticolae Hopk., and is an attempt to answer several questions which have arisen from the work of past investigators. The morphology of the organs is described and some interpretations of function are included.

Studies made by Hopkins (1915), Schedl (1931), Richmond (1935), Francke-Grosmann (1948, 1950), and Chapman (1958) suggest that much work needs to be done to clarify the terminology of some of the reproductive structures in scolytids, in the light of their functions. An example of this is the so-called seminal vesicle, found in many scolytids, but it is really an accessory gland. Progress of the study of fecundity (Reid, 1958b, 1962b) of the mountain pine beetle has been hindered by the incomplete knowledge of the functions of the bursa copulatrix, female accessory glands, egg fertilization, and ovulation. These events can only be interpreted with an understanding of the internal micromorphology as well as the conditions which help to produce them. Reid (1962b) has also shown that the behavior associated with mating and egg-laying is extremely variable and that adult activities on the host tree are delicately in balance with the environment. The sensitivity of this insect in the natural habitat is strongly reflected in internal changes. This study not only contributes some specific knowledge on reproduction in the mountain pine beetle, but it should have application to scolytids generally.

LITERATURE REVIEW

(a) GENERAL

The reproductive systems of insects have long been the subject of investigation (Malpighi, 1669; Swammerdam, 1737; Hunter, 1792; Harold, 1815; Dufour, 1825). This work describes the anatomical features of reproductive systems and correlates many activities of adult insects with reproductive functions. Much of our present understanding of the phylogeny of insect groups stems from such studies; the genitalia, especially of male insects, have long been widely used as taxonomic characters.

Many attempts were made by early workers to establish a clear phylogenetic pattern of development of the reproductive structures throughout the class Insecta (Crampton, 1929; Snodgrass, 1931, 1933, 1936). Subsequently, it has been necessary to understand the evolutionary mechanisms involved and to homologise the various reproductive structures. Snodgrass (1931, 1933) and Matsuda (1958) discussed the theories proposed by earlier workers in summarizing discussions on the morphology of the abdominal appendages of insects. From these discussions there appear to be two main theories for the interpretation of these appendages, Heymons' theory and the limb theory. Heymons' theory suggests that the genital processes are secondary integumental outgrowths from the sternal region and that they bear no relation to the true appendages. According to this theory only cerci and styli are homologised with true appendages. Few workers have given support to Heymons' theory; among them

[illegible]

(a) [illegible]

[illegible]

were Heberdey (1931), Friedmann (1934) and Matsuda (1958). In his review of the subject, Matsuda maintained that the evidence from postembryonic studies, favors a sternal origin for the external genitalia of insects. In all male insects the origin of external genital structures such as the penis and parameres can be traced from a pair of small ectodermal outgrowths which appear in the nymph or larva (Snodgrass, 1935, 1957). Furthermore, Snodgrass concludes that no convincing anatomical evidence is available that relates the penis or parameres to ninth segment appendage rudiments. On this basis he presented a simplified anatomical plan of the male genital apparatus for most pterygote insects which is consistent with a basic plan found in Thysanura, especially in Machilidae and in Lepismidae. This plan provides a fairly uniform interpretation for the major structures of the male insedt genital organs (Snodgrass, 1957). It is generally accepted that the primary external organs of male pterygote insects occur medially on the venter of the ninth abdominal segment, while in females the genital segment can be either the eighth or ninth.

Homologies of the female ovipositor are better understood (Michener, 1944; Gustafson, 1950). According to Michener the ninth abdominal appendages of the male insect can be homologised satisfactorily with the female ovipositor, also of the ninth segment.

The nomenclature of the insect ovipositor has been revised recently by Scudder (1961a, 1961b). In this revision the scheme of nomenclature of the pterygote ovipositor is based

were Mooney (1940), Rivlin (1956), and Ericksen (1956).

In his review of the subject, Ericksen mentioned that the existence theorems pertaining to finite, large, and infinite deformations in isotropic elastic solids, leaving a material model for the material problem in hand. He did note however the existence of several limited elastostatic solutions for finite deformations of an isotropic elastic cylinder or sphere, which were derived from a pair of linear partial differential equations which resulted in the theory of linear elasticity (Ericksen, 1956, 1957). Furthermore, Ericksen concluded that a particular elastostatic solution is valid if the material is a member of a particular class of isotropic materials, and if the boundary conditions satisfy certain specific necessary conditions. In a 1957 paper Ericksen discussed a particular class of isotropic materials and the class of boundary conditions for which the finite elastostatic solutions of the theory of linear elasticity are valid (Ericksen, 1957). It is worthwhile to mention that the linear elastostatic solutions of the theory of linear elasticity are valid for the class of isotropic materials and the class of boundary conditions for which the general solutions can be solved for arbitrary displacements.

Considerable of the recent literature has been concerned with the theory of finite elastostatic deformations (Ericksen, 1957; Ericksen and Rivlin, 1954). Some of the literature is still concerned with the theory of finite deformations of isotropic elastic solids, and the theory of anisotropic elastic solids, and the theory of the finite deformations of the finite elastic cylinder, sphere, and of the finite elastic beam.

The theoretical work in the theory of elastostatics has been concerned primarily with the theory of linear elasticity. In this theory, the problem of compatibility of the deformation components is solved

on the structural plan of the ovipositor found in Lepismidae. Snodgrass (1933) had based his interpretation of the ovipositor on the condition found in Machilidae. Scudder showed that the parts of the ovipositor could be homologised in all orders possessing genitalia developed on abdominal segments eight and nine. The gonangulum, a newly named sclerite, is essential for these homologies. Both structure and function of this sclerite were considered.

Several general reviews were found helpful in relating the morphology of the reproductive structures in Dendroctonus with their functions. The first reviews to be considered are those of Imms (1957) and Bonhag (1958). They described the known types of ovarioles found in all insect groups. The most primitive or panoistic type of ovariole has been recorded in Thysanura, Orthoptera, Isoptera, Odonata, Plecoptera, and Siphonaptera. More advanced types of ovarioles are polytrophic and telotrophic. The polytrophic type is represented in some Dermaptera, Psocoptera, Anoplura, Mallophaga, Coleoptera - Adephaga, Lepidoptera, Diptera, and Hymenoptera. This type has also been reported in Neuroptera with the exception of Sialis (Bonhag, 1958). The typical telotrophic ovariole has been found in Hemiptera (Bonhag, 1953; Davis, 1956) but it is also characteristic of Sialis and of Coleoptera - Polyphaga (Krause, 1946; Bryan, 1954; Schlottman and Bonhag, 1956; Zacharuk, 1958a). Wigglesworth (1953) states that the Adephaga exhibit the telotrophic condition while the Polyphaga have polytrophic

ovarioles. This is the converse of the more widely accepted view of Bonhag (1956).

Another important aspect of function is covered in the reviews by Khalifa (1949) and by Davey (1961). They add to the subject of spermatophore production and bring this up to date for all insect groups. Specific accounts of spermatophores in insects are given by Blunk (1912), Cros (1924), Davey (1956), and Fisher (1959). Knowledge of spermatophores is scanty, but their occurrence is known to be sporadic, even within a family.

Finally, Shteinberg (1960) discussed the possible adaptive features in the structure of the female ovaries of insects. He showed that there is variation in the number of egg tubes in different groups and sometimes even in the same species. Shteinberg stated that seven pairs of segmentally arranged ovarioles or testes must be regarded as the primitive gonad structure and that in most winged insects the number of ovarioles and the number of sperm tubes in the testes must have been secondarily modified, either by the process of "oligomerization" or by "polymerization". The significance of these processes as adaptive features can be more fully realized when we consider that an increase in the number of ovarioles may be a principal method of increasing fecundity. On the other hand, with a reduction in the number of ovarioles there can be an increase in the number of egg follicles. Regulation of the rate of growth of oocytes may also be an adaptive feature.

(b) COLEOPTERA

Our knowledge of the reproductive organs of Coleoptera has accumulated from many fields including taxonomy, morphology, and physiology. The work of Stein (1847) represents one of the first extensive investigations of the beetle ovary. He studied the internal sex organs and glands of female beetles, both anatomically and histologically. Escherich (1894) and Bordas (1900) (Deegener, 1928; Imms, 1957) investigated the testes and accessory glands and divided the Coleoptera into groups according to the complexity of testes structure. Sharp and Muir (1912), Muir (1918, 1920), and Sharp (1918) dealt with the structure of the male ejaculatory duct and external genitalia in many families. Tanner (1927) studied the female genitalia of 125 genera from 66 families. He concluded that 10 segments were present in the abdomen of most female beetles and that the eighth, ninth, and tenth segments and their appendages form the genitalia. According to Tanner, the appendages have been lost from the eighth and tenth segments but have persisted on the ninth. He termed these genital appendages the coxites, styli, and valvifers and was able to homologise them for all of the 111 species illustrated. Tanner divided the Coleoptera into three suborders, Adephaga, Polyphaga, and Scarabaeiformes, on the basis of characters of the female genitalia. Within the Scarabaeiformes he included the Scarabaeidae and Scolytidae and stated that these were the most specialized of the families studied.

[illegible]

Many workers have studied the development of beetle reproductive organs. These include Singh Pruthi (1924a, 1924b), Metcalfe (1932), Hodson (1934), Snodgrass (1935), Michener (1944), Wood (1952), and Zacharuk (1958b). Their conclusions showed that the penis is derived from the body wall and that the components of this organ cannot be related to the gonopods. The testes at least, were found to be of mesodermal origin, while the ejaculatory duct is of ectodermal origin. There seems little disagreement on the derivation of the structures of the female ovipositor. Singh Pruthi (1924b), Metcalfe (1932), and Zacharuk (1958b) agree that it is derived primarily from the gonopods of the ninth segment.

Williams (1945) described the internal genital structures, including associated glands of several species of male and female beetles, representing 12 families. The listing of ovariole numbers in 329 species, representing 45 families of Coleoptera by Robertson (1961) is also of importance, especially in the fields of taxonomy, evolution, and fecundity. Ovariole numbers in Adephaga were found to vary from 4 - 40, while in Polyphaga they ranged from 1 - 200. It was suggested that multiplication, reduction, and stabilization of ovarioles have occurred in the evolution of beetles.

An important publication which gives the principal terms used for the genitalia of male and female Soleoptera was presented by Lindroth and Palmén (1956). All principal terms used to identify the genital structures are defined and synonyms have been included.

Crowson (1960) discussed the phylogeny of Coleoptera. He dealt with their taxonomic position and grouping and supported his views with evidence accumulated from the fields of taxonomy, morphology, ecology, physiology, and paleontology.

(c) SCOLYTIDAE

Contributions to the taxonomy of bark beetles found in Europe, using characteristics of the male and female reproductive organs, were made by Nüsslin (1911, 1912) and by Lindemann and Fuchs (Hopkins, 1951; Francke-Grosmann, 1948, 1950). Nüsslin's classification was based upon characteristics of the ejaculatory duct, testes, seminal vesicles, vas deferens, and mucous glands of the male, while in the female the cement glands, bursa copulatrix, and the spermatheca were used. Several characteristics of the female organs were found to be consistent for the scolytids. These are, (1) the absence of a true ovipositor, (2) two ovarioles per ovary (see also Robertson, 1961), and (3) the presence of paired or single cement glands in most species. In addition, the bursa copulatrix is absent from only a minority of the scolytids.

Only one species of Dendroctonus in Europe has been described; D. micans Kug. The reproductive organs of this beetle were illustrated by Lindemann (Francke-Grosmann, 1948, 1950), Nüsslin (1911, 1912), and were treated in greater detail by Francke-Grosmann, (1948, 1950).

In North America significant taxonomic contributions on

bark beetles were made by Hopkins (1909, 1915), Swaine (1918), and Chamberlin (1939, 1958). In addition, revisions of the Ips (by Hopping) and Dendroctonus (by Wood) species of North America are being prepared.

Hopkins (1909, 1915) described the external morphology of Dendroctonus valens Leconte in detail and illustrated the general structures of the male and female organs of reproduction. Richmond (1935) carried out a similar investigation on D. monticolae. The reproductive structures of D. pseudotsugae Hopk. were partially illustrated by Atkins and Chapman (1957) and by Ryan (1959). Several references describing the genital organs of curculionid species were found helpful since their organs resemble those of Dendroctonus. Specific studies of curculionids include those of Hopkins (1911), Munro (1914), Bissel (1937), and Burke (1959).

The mountain pine beetle has received considerable attention, both in the United States and in Canada. In 1909 Hopkins gave a brief description of its life cycle and general distribution. Later workers including De Leon et al. (1934), Evendon et al. (1943), Hopping (1946), Hay (1956), Reid (1958a, 1958b, 1961, 1962a, 1962b), and Shepherd (1960 - 61), have studied many aspects of this timber pest, including seasonal history, biology, habits, and control. Reid (1958a, 1958b, 1961, 1962b) placed considerable emphasis on the internal changes in the female beetle which he related to egg-laying, mating, flight, and inner bark and wood moistures.

MATERIALS AND METHODS

The beetle material used in this study originated from naturally infested areas near Invermere, British Columbia. Mountain pine beetles were collected from lodgepole pine, *Pinus contorta* Dougl. var. *latifolia* Engelm., during the summers of 1960 and 1961. Two methods were found useful for rearing them artificially in the laboratory.

Sufficient beetles were introduced onto freshly cut pine logs of convenient lengths to infest each with several active pairs. While introducing them a net cage was placed over the log to ensure maximum infestation. This procedure was most effective when carried out in darkness. To obtain large broods by this method it was essential to retain as much of the inner bark and wood moisture as possible and loss of moisture was minimized by applying a coat of wax to the exposed cut ends of each log.

Infested logs were usually stored at room temperature and under these conditions one complete life cycle could be obtained within six to eight weeks. Adults emerged over a period of several days. Thus fresh specimens were available almost daily. Also, female beetles in different stages of maturity could be dissected and compared with females from naturally infested trees.

The second method used was more refined and has been described in greater detail by Reid (1962b). Fresh inner pine bark was held tightly between two transparent sheets of plastic.

Waterproof tape was applied around the edges of this sandwich-like unit to keep moisture loss to a minimum. Reid has termed the completed unit of bark tissue, plastic, and tape an observation plate. It allows direct observation of activity within the plate at any moment. A small half inch by one-eighth inch groove was cut at one end of the bark, into which the female beetle was placed. The male was usually inserted one day later. This method of rearing was limited to the study of adult activity while in the host tissue since the bark did not retain sufficient moisture and food for larval development. However, mating, gallery excavation, and egg-laying appeared to proceed normally as long as the bark remained in a moist condition.

Observation plates were of two sizes, $2\frac{1}{2}$" x 3" and $2\frac{1}{2}$" x 6". The smaller were convenient for studying the mating process, the larger for egg-laying activities. Temperature and bark moisture could be controlled more precisely than in previous method.

Beetles were removed from the observation plates when in various stages of activity during the interval from mating to egg-laying. This allowed observation of the development of the internal reproductive systems. Once the appropriate stage occurred, the plate was immediately opened and the insect was either placed in fixative solution or dissected in physiological saline (Ringer's solution). The fixative used for all histological tissue preparations was formal saline. Copulating pairs were successfully preserved by immersion in boiling formal

saline for one or two seconds.

Many observations were made on the reproductive system while dissected in physiological saline. In the female beetle contractions of the median oviduct and bursa copulatrix often continued after dissection. Mass movement of the spermatozoa within the spermatheca could also be detected and this was useful for separating mated from unmated females. In the male similar contractions were noted during the functioning of the ejaculatory duct and at such times the secretion of accessory gland fluid was studied in relation to the funnel mechanism.

Specimens for histological study were selected when in various stages of activity. These stages apply particularly for the female beetle and are listed below.

(1) Newly developed adults.

(2) Adults during the flight stage.

(3) Females during egg-laying and gallery construction.

(4) Adults in the overwintering condition.

Sometimes only the reproductive system with its posterior attachments and sometimes the entire metathorax and abdomen were fixed. The latter was preferred since there was no risk of damage. The tissue was then dehydrated and embedded in wax (melting point 60 - 62° C.) according to the procedures outlined in Davenport (1960). Serial sections were made at six and eight microns. Two hematoxylin solutions were used, Delafield's (Davenport, 1960) and Heidenhain's (Pantin, 1960); both gave satisfactory results. All sections were counterstained with eosin Y which showed an affinity for muscle tissue, yolk,

and cytoplasm.

In addition to the sectioned material, many whole mounts of the reproductive systems were prepared in a water mounting medium (Gurr's); others were dehydrated, cleared in cedarwood oil, and mounted in Fisher's Permount. Cleared mounts stained with eosin Y gave the best results for determining the muscle attachments of the reproductive accessory parts.

All drawings were made to scale using a calibrated micrometer eyepiece and a camera lucida.

RESULTS

(a) GENERAL MORPHOLOGY OF METATHORAX AND ABDOMEN

The combined abdomen (Abd) and metathorax (Metath) form a cylindrically-shaped unit, and as in many scolytids, the abdomen tapers rather abruptly (fig. 1). The male reproductive system lies entirely within the abdomen and occupies a dorsal position (fig. 1). In a newly developed female the position is similar except that the ovaries (Ov) extend slightly into the metathorax and are suspended from the prephragma (Preph) as shown in fig. 1. As egg development advances the terminal portions of the ovaries move nearer to the prephragma.

According to Richmond (1935) the prephragma of the metathorax bends ventrally and has two sclerotized lobes which are divided medially by a small notch. On the dorsal margin of this notch are attached the two suspensory ligaments (Reid, 1958a) which suspend the anterior end of the ovaries (fig. 1; Suslig). There are no similar suspensory attachments found in the male beetle. Dorsal to the suspensory ligaments and the terminal portions of the ovaries are three pairs of dorsal longtitudinal flight muscles which undergo autolysis during vitellogenesis (Reid, 1958a; Atkins and Farris, 1962). The tergosternal flight muscles change similarly and this provides more free space for the ovaries to expand during egg development. At the same time extra space is made available for the expansion

(*) [illegible]

of the proventriculus since the egg-laying period is concurrent with feeding.

The abdomen is of a cryptogastran type (Imms, 1957) and consists of terga (T) I to VIII and sterna (S) III to VIII (fig. 1). Sternites 1 and 2 are apparently fused to sternite 3 and are concealed within the hind coxal cavities (Richmond, 1935).

Tergite 7 is a prominent sclerite in both sexes and carries one of the few externally visible sex characters. Two small stridulatory scrapers project from the posterior point of this sclerite in the male and these provide the only convenient means of separating the sexes while alive. The eighth tergite is more conspicuous in the male while in the female it is partially covered by the seventh tergite. In both sexes, however, the eighth sternite is much reduced, and except for brief moments during mating or egg- laying, it is completely concealed by the eighth tergite and seventh sternite. The eighth sternite in the male is more heavily sclerotized laterally than medially (fig. 12). In the female the sclerotization is similar except that the median portion has become entirely membranous (fig. 19). The thickened lateral portions of the eighth sternite serve as points of attachment for strong muscles which extend ventrally to the seventh sternite. These muscles allow a teloscopic movement of the posterior abdominal segments.

The terminal portions of the reproductive systems are

intimately supported from tergum VIII and sterna VII and VIII by muscle and membranous tissue (figs. 12, 21). These three regions form the posterior enclosure of the genital opening (GenOp) and anus (figs. 2, 19, 21). The genital opening of both male and female is ventral to the anus.

The female reproductive organs are also held in position by a network of tracheal branches, most of which arise from the abdominal spiracles. This network is most conspicuous on reduced ovaries as compared with ovaries expanded with mature eggs. The tracheae are also most numerous near the base of the ovarioles and their attachment probably never extends any deeper than into the epithelial sheath of the ovarioles (Bonhag and Arnold, 1961). Thus, an important secondary role in the tracheae may be a mechanical one, i.e., to keep the ovaries in a stationary position in the dorsal half of the abdomen, especially during the contractions of the median oviduct. Tracheation to the male reproductive system was less noticeable.

(b) MALE REPRODUCTIVE SYSTEM

(i) General: The male organs in the mountain pine beetle (Richmond, 1935) correspond closely to those of *D. valens* (Hopkins, 1915), however, several differences were revealed by the histological studies. Figure 1 is a lateral view of the reproductive system and shows the position occupied within the abdomen. A more complete representation of all parts is given in figure 2, but in a ventral view.

The male reproductive system includes the following major

components. There are two testes (Tes) each linked to a short vas deferens (Vd) and at the posterior end of each vas deferens are two pairs of accessory glands (AcGl) and possibly a third (X) (figs. 4, 5). A pair of seminal ducts (SmlD) extend from the glands to unite medially with the ejaculatory duct (EjD). This duct then continues posteriorly to fasten onto the internal intromittent organ or penis (Pen). When in the normal position the penis lies withdrawn in the abdominal cavity (fig.2).

(ii) Testis and vas deferens: The testes are depicted in figure 2 and in greater detail in figures 3, 6, and 7. They are usually bean-shaped, whitish structures, dorso-ventrally flattened, and measure approximately 0.8 mm. at their maximum width. Each testis is divided into six compartments, all of which are similar in size. These are termed the testicular follicles (fig. 3; Fol). From a median point on the testis the vas deferens (fig. 3) projects posteriorly and is at first a broad tube which tapers to the size of the ejaculatory duct. Within each testis, the vas deferens divides into two short ducts, the vasa efferentia (fig. 3; Ve), and three follicles appear to be continuous with each vas efferens.

An epithelial sheath (fig. 3; EpSh) forms an outer covering over the testis. This sheath varies in thickness at various points but is thickest around the base of the vas deferens. At this point it appears to continue as an outer sheath over the vas deferens but becomes less thick. This epithelium is also continuous with the septa (fig. 3; Sep)

[illegible]

(ii) [illegible]: [illegible]

[illegible]

[illegible]

[illegible]

which separate one follicle from another. The epithelium has the appearance of a loose reticulate membrane with numerous oval-shaped nuclei. The epithelial sheath rests on a basement membrane.

Within the follicles the sex cells occur in different stages of development, and for the insect testis in general, four zones of development have been described. These are, the germarium zone, the zone of spermatocytes, the zone of maturation and reduction division, and the zone of transformation (Wigglesworth, 1953). In the testis of the bark beetle only the last zone could be distinctly identified. This was observed near the base of each follicle or at the anterior end of the vasa efferentia. Towards the outer periphery of the testicular follicles the sex cells were of several sizes. At least three sizes could be distinguished with groups of each size often found in a cluster (fig. 3; Nuc). It may be assumed that these nuclear bodies represent the first three zones of development with the earliest stage occurring at the outer extremity of each follicle. Development of the spermatozoa appears to progress at the same rate in all follicles.

The young spermatozoa near the base of each follicle are enclosed in sperm cysts (fig. 3; SpCst). According to Imms (1957) these cysts are composed of special cyst-cells which enclose and probably nourish the immature spermatozoa until they mature. At the completion of development the cyst-cells apparently rupture, spilling the mature sperm into the vasa efferentia.

In histological preparations of males that were removed from the host tree in late November, large irregular shaped bodies were observed at the base of the testicular follicles. Intermixed with these bodies was a granular material which showed a strong affinity for eosin. The dark bodies appeared to have their origin from the wall of the vas efferens. Moreover, their shape and coloration seemed identical with the prominent nuclei of that region. The granular material, on the other hand, probably originated from the inner wall of the vas efferens since identically stained material was observed within oval-shaped bodies in the walls of these ducts. This phenomenon did not occur in the same magnitude in all other sectioned males which were collected while in their normal summer activities.

Both the vas efferens and vas deferens are thick walled tubes having an inner lining of epithelium with cyloplasmic processes (fig. 3; CytoPr) and prominent nuclei; an outer epithelium occurs on the vas deferens only. The inner layer shows acidophilic properties while the outer has a strong affinity for hematoxylin. The anterior portion of the vas deferens is widened and this portion may be termed the true seminal vesicle (fig. 3; Smlv). The vasa efferentia also function for sperm storage but their holding capacity is much less. Large masses of sperm are always found in these two ducts when the males are fully mature. The posterior end of the vas deferens leads into the funnel mechanism (fig. 4; Fun).

Workers in the past have referred to the most posterior accessory gland (figs. 4, 8; AcGl(b)) in male bark beetles as the "seminal vesicle" (Hopkins, 1915; Richmond, 1935; Chapman, 1956), however, no evidence was found to support such a conclusion in D. monticolae. Chapman (1956) separated sexually mature males of Trypodendron lineatum (Oliv.) from young males on the basis of sperm accumulation in the vasa deferentia. Of the "seminal vesicles" in T. lineatum, he stated that sperm were never found within them. Francke-Grosmann (1950) reported that the vasa deferentia in D. micans also perform the function of seminal vesicles (Samenblase).

Within the testes of the mountain pine beetle, apparently three follicles feed mature spermatozoa into each vas efferens and a pair of these ducts are present entirely within each testis. There is some variation in the morphology of the testes and vasa efferentia between other Dendroctonus species. In D. micans, the vasa efferentia are visible external to the testes (Francke-Grosmann, 1950) and each testis is a single unit. In D. valens the vasa efferentia are arranged identically but each testis is subdivided (Hopkins, 1915). The structural arrangement in the Douglas fir beetle, D. pseudotsugae (Ryan, 1959) appears to be identical with the arrangement in the mountain pine beetle. Some peculiarities have also been observed in the testis structure in the mountain pine beetle. In most dissections, the testes appeared as illustrated in figure 2. However, on rare occasions, divided testes were found where

short vasa efferentia were visible and external to each half testis. It is presumed that in such occurrences, the testis is equally divided with three follicles per half. Richmond (1935) in his study of D. monticolae illustrated the testes as described in the rare condition.

(iii) Accessory glands: Two pairs of accessory glands will be described below and are labelled AcGl(a) and AcGl(b) in figures 2 and 4. In addition, a third structure (fig. 4; X), also believed to be glandular, will be discussed.

Accessory gland (a) (AcGl(a)): These glands are worm-like in form and appear as uniform tubes for their entire length. They are usually coiled as shown in figure 2. At a point near their mid-length a short duct (figs. 5, 9; AcGl(a)D) extends posteriorly to form a connection with the funnel opening. Laterally from the short duct the two end portions of the gland extend posteriorly within the abdomen. In most freshly dissected mature males the glands are milky colored. In many newly developed males on the other hand, they are almost transparent, thus suggesting a ripening with maturity. In both age classes of males, however, there appeared to be little or no difference in their overall size. When live males with transparent glands were dissected in Ringer's the glands were easily ruptured. On such occasions the transparent fluid flowed out as a viscous material in thread-like manner. Once in contact with Ringer's, it hardened somewhat and exhibited slight elastic properties. It is heavier than water and when in contact with

this, it becomes milky in appearance. Once in the milky condition it appears slightly granular and is fairly refractive. When male beetles have been stored in formal saline fixative for some time the fluid of these glands turns a rust color. Several similar properties have been recorded for the male accessory glands in Popillia japonica Newman by Anderson (1950).

Histologically, accessory glands (a) and the fluid within appear to be uniform over their length. The wall of this gland is thick and has prominent nuclei (fig. 4). The glandular secretion possesses acidophilic properties. During mating this gland contributes the largest component of the secretion.

Accessory gland (b) (AcGl(b)): In the mountain pine beetle this gland is a prominent structure (figs. 2, 4, 8, 9, 10). It has been described as mellon-like in shape and often has four well defined lobes. These lobes, however, do not divide the gland into different sections; the interior is a single cavity. This gland is constructed to serve a dual function. Besides being glandular, it holds the posterior tip of the vas deferens in proper alignment with the seminal duct. It varies considerably in size, depending on the age and activities of the animal. Maximum widths measured in the transverse plane vary from 0.3 to 0.7 mm.

In freshly dissected material the glands are nearly transparent, while the fluid content is completely colorless. Although no attempt was made to determine the properties of

this fluid, it appeared to be miscible with water. Chapman (1956) states that in the ambrosia beetle, T. lineatum the contents of this gland are clear except for small amounts of oily material. At no time did he observe any other materials in this gland, in spite of the close association of its opening with spermatozoa and fluid from the worm-shaped glands. In D. micans, however, Francke-Grosmann (1950) reported small clumps of such mixture within accessory gland (b), but this was very seldom. No extraneous material was ever observed in accessory gland (b) of the mountain pine beetle.

The histological structure of accessory gland (b) is similar to that observed in the (a) glands. The wall is composed of a thick layer of secretory cells which have large nuclei (fig. 8; Nuc). In several histological preparations small spherule-like bodies were observed adjacent to the inner gland wall; this was probably an oily material similar to that observed by Chapman (1956). The interior of the glands rarely stained.

X-structure: This small structure lies almost hidden below the worm-shaped accessory gland, but it feeds into the main sperm channel in the same manner as the vas deferens and the (a) glands. It is illustrated in figures 4 and 5. In fresh preparations the outer bulb portion of this structure has a yellowy appearance and in transverse section (fig. 5; X) its wall is thin, rigid, and nucleated. Within the bulb portion an acidophilic substance shows clearly. Posterior to the bulb is

a short duct. Its wall appears to be identical in cellular structure to its two neighboring ducts, the vas deferens and the duct of accessory gland (a). The wall is thick with an inner layer of epithelial cells and an outer layer which may be partly muscular (fig. 9). Prominent nuclei are characteristic in the outer layer. The duct opening from the X-structure is small in comparison to the openings from the two adjacent ducts (fig. 9).

No similar glandular structure has been recorded in other bark beetles. However, according to Imms (1957) three pairs of accessory glands are not uncommon in the Polyphaga. As in the original observations of Escherich (1894), male accessory glands have been described according to their origin. Those glands which are derived from the mesoderm and formed as evaginations of the vasa deferentia have been termed mesadenia, those of ectodermal origin and which arise from the ejaculatory duct as evaginations are termed ectadenia. If this sytem of nomenclature can be applied to D. monticolae, then the (a) glands and X-structure would probably be mesadenia while the (b) glands would fall into the ectadenia group. Francke-Grosmann (1950) suggested the name "middle gland" for the (b) gland because, as she states, "it connects the ectodermal ejaculatory duct with the mesodermal vas deferens".

All male glands, including the vas deferens, open into the ejaculatory duct system at the same point. This is brought about by the arrangement of the ducts of each gland in relation

to the funnel mechanism or widened anterior end of the seminal duct (fig. 4). Three ducts (AcGl(a)D, Vd, X) form a tri-duct system and these in turn are surrounded by the circular opening from the (b) gland. It appears, therefore, that an intermixing of four materials takes place simultaneously.

In figure 4 accessory gland (b) is illustrated with its opening continuous with the funnel. Opening and closing of this gland is brought about only when contractions of the seminal and ejaculatory ducts occur, as observed when dissected in physiological saline. The fluid from the accessory (a) gland is readily recognized and during contraction of the ejaculatory duct system, quantities of this fluid can be seen to pass into the funnel with each successive contraction. It would seem that the contracting movements of the associated ducts, especially the seminal and ejaculatory, would ensure a mixing of the glandular secretions in fairly constant proportions. This mixture containing spermatozoa intermixed with glandular fluids constitutes the spermatophore when deposited in the female beetle during copulation.

With regard to the functions of the accessory gland (b) (Samenblase) in D. micans, Francke-Grosmann (1950) suggests that this gland contributes a secretion which envelops the mixture of sperm and fluid from the (a) glands to form a so-called "spermatophore". However, in the mountain pine beetle the properties of the fluid from the (b) glands are not understood and since the sperm packets so far observed have been

more or less spherical objects, it would appear more likely that this fluid is fully intermixed with each spermatophore.

(iv) Ejaculatory duct: The ejaculatory duct system forms the main tubular pathway from the testes to the exterior of the abdomen. It extends from the accessory glands posteriorly to the internal accessory apparatus of the copulatory organ (fig. 2). For convenience the two anterior branches of the ejaculatory duct have been termed seminal ducts, however, their function and histological structure appears to be identical with the median ejactulatory duct proper (fig. 12A, B). In cross-section the ejaculatory duct displays a thick layer of circular muscles and an inner epithelium (fig. 12B). The nuclei of the inner wall of this duct are more numerous and are larger than the nuclei of the muscular layers. No distinct intima was observed lining the inner epithelium.

(v) Genital apparatus: The male genital organ of the bark beetle is a rhyncophorus type (Sharp and Muir, 1912) and is illustrated in various aspects in figure 11A, B, and C. It is the intromittent organ used for conveying the male reproductive secretion products to the female during coition. This organ with some of its anterior musculature was briefly described by Richmond (1935) and the male genitalia of D. valens (Hopkins, 1915; Bruhn, 1947) is similar in nearly all respects. However, greater detail is presented here on the morphology of structures and some differences of interpretation are included.

The major portion of the genital organ is sclerotized as

shown in figure 11A, B, and C. These parts include the median penis (Pen) with its paired anterior apodemes (Apod) and an internal accessory apparatus consisting of seminal rod (SmlRd) and anchor (Anch). The tegmen (Tgm) and spicule (Spcl) are also accessory parts of the genitalia but are separate sclerites and may be attached to the penis indirectly by muscle or membranous tissue. In addition to these sclerites, the internal sac (IntSa) is also an important membranous component of the penis. It is normally folded within the penis, but during mating it becomes everted as in figures 13 and 14.

The penis is tubular in form with a basal orifice (BOr) at its anterior end and an ostium (Ost) at its posterior apex (fig. 12). Two heavily sclerotized apodemes extend anteriorly from the lateral walls of the main penis body. These serve as points of attachment for muscles connecting to all of the accessory sclerotized parts of the penis except the spicule. On the dorsal aspect of the penis two prominent lobes are present; these were termed lateral folds by Hopkins (1915). A median portion of this aspect is also membranous and this may correspond to the first connecting membrane (figs. 12, 13, 14; ConnMm[1]) after Metcalfe (1932). It attaches from the basal orifice rim to the posterior of the abdomen. A second membrane or a continuation of the first connects the penis to the tegmen. When the penis is in the normal position the first connecting membrane forms an outer sheath and when forced external to the abdomen, the anterior of the penis merely slips through this

membrane, thus pulling it inside out.

Three sensory areas occur on the penis, one at the ventral apex and two on the dorsal lobes. These sensory structures are in the form of short conical spines (figs. 11A, B, 18; SensPen) and probably function as tactile receptors.

The internal accessory apparatus is fixed in position to the inner dorsal wall of the penis, near its posterior apex. At this point the posterior sides of the anchor articulate with the terminal infolded portions of the penis wall.

The internal sac is connected to the arms (Arm) of the anchor in such a manner that the entire accessory apparatus lies on the inner lining of the sac. With this arrangement the ejaculatory duct remains external to the sac, except for its terminal end, which is rigidly attached to the anchor and rod. In addition, the internal sac is continuous with the internal apex of the penis.

The internal accessory apparatus appears to serve three functions. Firstly, it provides the posterior support for the ejaculatory duct. Secondly, it is rigidly fixed to the penis, yet is movable in a hinge-like manner. With these features the gonopore can be properly orientated with the exterior of the penis. A third function is provided by the seminal rod which acts as a guide for the seminal fluid (fig. 16) during ejaculation. Hopkins (1915) described the accessory apparatus in D. valens as serving a valvular function but this was

earlier doubted by Sharp and Muir (1912). No histological evidence was found in the mountain pine beetle to suggest a valvular function for any part of the seminal rod or anchor. Moreover, the posterior ejaculatory duct does not attach onto the anterior end of the accessory apparatus as suggested by Hopkins (1915) and Richmond (1935), but rather to a more median point on its dorsal side. The attachment appears to be more firmly held to the arms of the anchor than to the seminal rod (fig. 16). This arrangement corresponds closely to the condition reported for D. micans (Francke-Grosmann, 1948). The gonopore (Gpr) for the posterior ejaculatory duct opening lies between the arms and seminal rod (figs. 16, 17B).

The overall form and structure of the internal sac can be properly visualized only when everted in position for mating (figs. 13, 14). When fully everted it appears as a thin, almost transparent membrane which has a large median lobe that is partially bisected from the dorsal side and two prominent lateral lobes (figs. 13, 14; LLb, MLb). On the outer surface of the lobes two patterns of spiny sclerites are present. The lateral lobes display an even distribution of small conical spines (figs. 13, 14) which are arranged individually, while the larger median lobe possesses a series of small rows of spines. The latter spines are smaller than those of the lateral lobes and become progressively smaller towards the posterior tip. The individual rows appear evenly spaced and are arranged transversely over this lobe. No sclerotizations

were observed on the ventral side of the median lobe.

At the very posterior tip of the median lobe is a small circular structure (figs. 14, 15; Y) which is yellowish in color when seen exteriorly (fig. 14; Y). It is believed to be a sensory structure but may be glandular as well. In figure 14 it is shown in cross-section while the sac was retracted within the penis. Its outer wall is firm and may be partly sclerotized. Internally it is nucleated and some differentiation of the cytoplasm is suggested.

A similar structure was observed in D. micans by Francke-Grosmann (1948) to which she ascribed the term epithelial body. She believed it to serve some role in regulating blood pressure within the everted sac. No further studies were made, however, to confirm that such a function exists.

The tegmen is a shallow U-shaped sclerite located on the ventral side of the penis (fig. 11A, B, C, D, E) and is normally situated about two-thirds of the distance from its posterior tip. The tegmen forms a narrow band with its ends curved dorsally. Two small anterior projections are present in a median position (fig. 11B). Since the tegmen serves an important function for muscle attachment it never moves exterior to the abdomen during mating.

The most prominent accessory sclerite of the genital apparatus is the spicule (figs. 2, 11, 12). This structure has been termed variously but the term adopted here follows the definition given by Lindroth and Palmén (1956). It forms

a major support for the intromittent organ. In structure the spicule resembles a round bar, bent in the form of a double "U". The anterior end is slightly enlarged and rests in a median dorsal position with the apodemes (fig. 11C). From its anterior tip it extends laterally and posteriorly, then transversely near the posterior end of the penis (fig. 11A, B, C), thus forming a large "U". The transverse portion has two pointed ends which project dorsally on either side of the penis, forming a second, smaller "U". All three terminal points of the spicule play an important role for the attachment of the associated muscles. The spicule, unlike the tegmen, remains relatively stationary within the abdomen during the mating process.

(vi) Musculature of genital apparatus: All separate muscles which have been found on the male genital apparatus are recorded below as well as their points of attachment. For convenience they have been assigned numbers, ie., M_1 to M_{12}, and are illustrated in figures 11D, E, 12, 13, and 14.

The first six muscles (M_1 to M_6 inclusive) serve to hold the spicule in a stationary position within the abdominal cavity. M_1 and M_4 extend from the posterior points of the spicule to attach onto the inside lateral margin of tergum VIII. M_2 and M_5 also originate from the posterior spicule prongs but attach onto the inside margin of sternum VIII. M_3 and M_6 originate similarly to M_2 and M_5 but extend ventrally and posteriorly to sternum VIII.

[illegible]

(iii) [illegible]: [illegible]

[illegible]

M_7 is in the form of a band (fig. 11D, E). By attaching onto both posterior spicule prongs, it completes a ring around the posterior end of the penis. The first connecting membrane passes between this ring and the penis. Relaxation and contraction of this muscle band probably controls the rigidity of the intromittent organ when it is extended during mating activity. It also serves as a guide for the penis to slide through.

M_8 and M_9 also attach onto the spicule, although in function, the two oppose one another. M_8 is a large muscle (fig. 11D, E) which originates from the anterior end of the spicule and attaches onto the two lateral arms of the tegmen. In so doing M_8 and the tegmen form a loop around the apodemes. M_9, on the other hand, extends from the tegmen to the transverse portion of the spicule. It takes the form of a broad muscle band. When the genital organ is in the normal retracted position, this muscle is always partly relaxed while its opponent, M_8 is partly contracted (fig. 11D).

M_{10} is a small but important muscle which extends from the two anterior projections of the tegmen to the anterior tips of the penis apodemes (fig. 11D). The ejaculatory duct passes medially between this pair of muscles to enter into the penis tube. Part of the function of this muscle is for retracting the penis after copulation. It may also help to prevent lateral movement of the anterior end of the copulatory organ.

M_{11} and M_{12} function solely for the withdrawal of the

internal sac, after coition has taken place. M_{11} consists of two large muscles, each originates from the anterior tip of an apodeme. These two muscles extend posteriorly within the penis tube where each divides into at least three branches. One branch of each muscle attaches onto the anterior end of the internal accessory structure while the other two branches spread out over the interior lining of the internal sac (figs. 11D, E, 13, 14). M_{12} is also paired; one muscle is present within each lateral lobe of the internal sac. They extend from the inside of the lateral wall of the lateral lobes to the wall of the median lobe (figs. 13, 14).

(vii) Eversion of genital apparatus: The following description of the function of the male genitalia is based primarily on observations of the associated musculature when fixed in the mating position and when fixed in the normal retracted position. This account is similar to the observations and conclusions of Francke-Grosmann (1948) in her studies of the male genitalia of *D. micans*.

Beginning with the genitalia in the normal retracted position, the first changes likely to occur are the contraction of M_9 and M_{10}, with a simultaneous relaxation of M_8. Contraction of M_9 probably causes a slight counter clockwise rotation of the penis so that the gonopore can be orientated dorsally. The activities of these muscles project the penis posteriorly out of the genital opening, causing sufficient movement to bring the anterior tips of the apodemes in line with the

posterior transverse section of the spicule (fig. 12). At the same time the tegmen is pulled backward to the posterior end of the spicule (fig. 12). Projection of the penis is probably made easier with a relaxation of M_7 and the lateral muscles of the eighth sternum. The function of M_1 to M_6 inclusive may help to shift the spicule nearer to the posterior abdominal wall. The intromittent organ is now at maximum extention (figs. 13, 14) for mating.

A second series of events now takes place to unfold the internal sac. This unfolding appears to involve only the relaxation of M_{11} and M_{12} and it must be assumed that blood pressure plays the major role for sac eversion. As the sac is forced backward the infolded posterior sclerotizations of the penis fold out laterally, carrying the internal sac and the accessory apparatus posteriorly. This movement swings the seminal rod backward to a transverse position with the penis. Francke-Grosmann (1948) suggested that the stiffening and pumping action of the muscular ejaculatory duct also helps to force the accessory apparatus posteriorly. The internal sac then completely unfolds in balloon-like fashion, bringing the gonopore adjacent to a mid-dorsal point at the base of the median lobe (fig. 13).

During observations on the mating process, it appeared that the internal sac was completely everted only when in the genital chamber of the female. Retraction of the genital organ conceivably takes place in a similar manner as eversion but with the withdrawl of blood from the sac and the reverse

operation of the muscles; ie., M_{12} contracts first, followed by the contraction of M_{11} and so on until the relaxation of M_9 and M_{10}.

(viii) Changes in the male reproductive organs: Throughout the life cycle of the male adult bark beetle, few developmental changes were noted as regards the reproductive structures. Newly developed males, when they emerge from the brood tree, are apparently sexually mature; when young males are examined their testes always show some mature spermatozoa. It was noted by Reid (1958b), however, that young broods seldom mated before emerging from the host tree. Mated females were of the order of less than one per cent. In D. micans, Francke-Grosmann (1950) reported that the male beetle becomes sexually mature before its cuticle has completely darkened.

Histological preparations of the testes of newly developed mountain pine beetles revealed that the quantity of mature sperm increases for the first few days. After this period, and especially after mating, large masses of sperm may be found within the vasa efferentia and vasa deferentia. The only other variation observed in the reproductive system during the male beetle's life was the presence of dark stained bodies and granular material in the vasa efferentia as already described for the overwintering male.

An attempt was made to compare the size of the (b) glands and testes of newly developed (one day after emergence) males with the same structures in five days old (five days

after emergence) males. This was done by taking the average maximum width of testes and the (b) glands for each beetle and plotting the values obtained against total body length. The results are illustrated in chart 1. The relationship between the (b) gland of one day old and the (b) gland of five days old is a close parallel. A similar relation exists for the testes. Both structures show a small linear increase with increase in body length.

Characteristics of the (a) glands were also noted in the above two groups (40 beetles per group). The criterion used in comparing one group with another was based on the degree of transparency of the gland fluid. Three categories were used, transparent, slightly milky, and milky. For the one day old beetles, the ratio was 5:5:30 respectively, and for the five days old beetles, the ratio was 0:4:36. Males older than five days usually had milky colored accessory glands. Moreover, it was observed that when the fluid from the (a) glands was secreted during mating or lost from rupture while in dissecting solution, portions of the gland became almost transparent. Finally, the presence of gland secretion (fig. 16; AcGl(a)Fl) within the male genitalia was an indication that mating had taken place.

(c) FEMALE REPRODUCTIVE SYSTEM

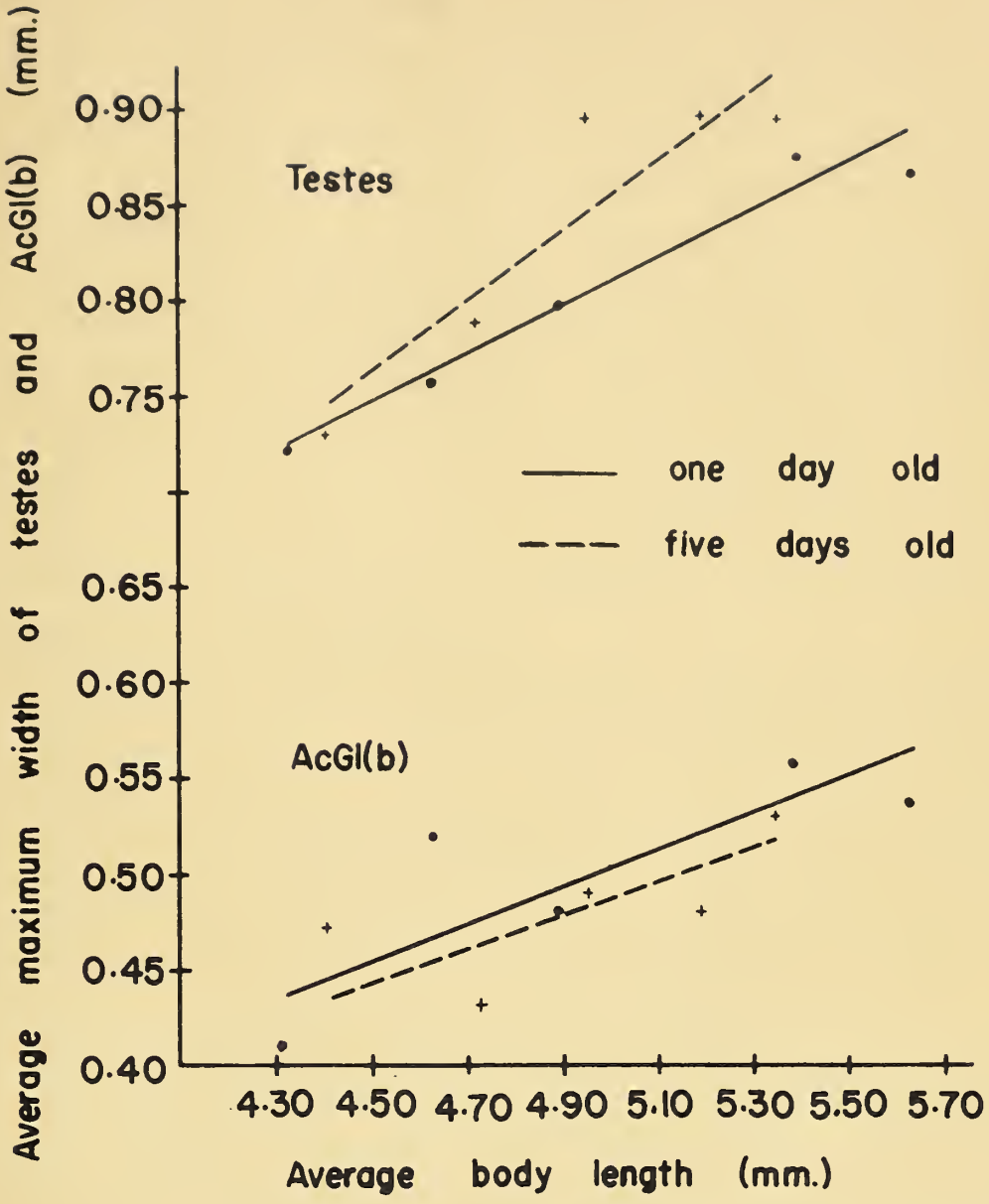
(i) General: The general structures of the female organs of reproduction in D. monticolae have been illustrated by Richmond (1935) and by Reid (1958a), however, some changes of

interpretation were found necessary.

All components of the female organs are illustrated in figures 19 and 20 and include two ovaries (Ov), each with a suspensory ligament (SusLig), a pair of lateral oviducts (LOvd), a median oviduct (MOvd), a prominent bursa copulatrix (Bcopx), a spermatheca (Spth), and a pair of accessory glands (AcGl). The median oviduct opens posteriorly via the genital opening (Figs. 19, 21A; GenOp). There are no accessory sclerites associated with the posterior end of the female reproductive system, nor with the posterior abdominal segments.

(ii) Oviducts: Included in the oviduct system are a common egg tube situated medially and two short lateral ducts which lead from the common duct to the ovaries. All portions of the egg tube appear to be similar in their muscular structure (fig. 23), except for the posterior region (fig. 21A). A transverse section of the median oviduct in the relaxed condition (fig. 23) shows an inner layer of longtitudinal muscles (LnMcl) surrounded by several layers of circular muscles (CMcl). When relaxed the inner wall is convoluted (fig. 23). In addition to the muscle layers, a thin cuticular membrane lining covers the inner wall of the lumen and carries numerous small spicules. These sclerotized spines project into the lumen with a posterior orientation, and are most numerous near the posterior end of the median oviduct. According to Jackson (1960) these spines are a characteristic feature of the Coleopteran median oviduct.

Chart 1. Relationship between body length of male *D. monticolae* and the average maximum width of testes and accessory glands (AcGl(b)). The dotted line represents five days old males which were stored with females and fresh inner pine bark; the solid line represents beetles one day old. A total of 80 beetles were examined, 40 in each age group. Each point on the chart represents an average of eight beetles which were arranged according to body length, from shortest to longest. All measurements are in millimeters.


Average maximum width of testes and AcGl(b) (mm.)
0·90
0·85
0·80
0·75
0·65
0·60
0·55
0·50
0·45
0·40
Testes
AcGl(b)
one day old
five days old
4·30 4·50 4·70 4·90 5·10 5·30 5·50 5·70
Average body length (mm.)

(iii) Copulatory pouch: The copulatory pouch is dorsal to the median oviduct and includes the vagina (Vag) and the bursa copulatrix (Bcopx). The genital opening is continuous with the copulatory pouch as well as the median oviduct (fig. 21A). Only a small portion of the bursa copulatrix is shown in the median view of figure 22A since the bursa characteristically curves to the left (figs. 19, 22A). The muscular wall of the vaginal region does not appear thick and may only consist of circular muscles on its dorsal side. The posterior musculature of the vagina is thickened and is arranged similarly as described for the posterior end of the median oviduct. Hence, the copulatory pouch may also be closed off from the posterior by a sphincter closing mechanism.

Surrounding the inner wall of the vagina and posterior end of the bursa copulatrix is a loose membrane (figs. 23, 25), to which are fixed numerous spicules, somewhat larger than those described for the median oviduct. They appear to be present only on the dorsal wall of the vagina and project anteriorly, in contrast to the oviduct spines.

The bursa copulatrix forms a dorsal diverticulum from the median oviduct, is blind at its anterior end, and is slightly longer than one millimeter. It is a muscular tube with essentially the same arrangement of muscles as the median oviduct. When in a relaxed state, the inner bursa wall is also convoluted. A thin membrane forms an inner lining for most of its length. Near the basal end of the bursa the muscular wall is slightly

constricted (fig. 22A), and immediately posterior to this constriction are two spiny sclerites (figs. 22A, B, 23; Scl). These lie on the dorsal inner wall of the bursa and appear to attach directly onto the muscle tissue (fig. 23). Movement of these sclerites takes place during contraction and relaxation of the bursa musculature. In cross-section these sclerites are somewhat convex and carry about ten well defined spines on their outer surface. These project inwardly and posteriorly within the bursa (figs. 22B, 23).

The occurrence of similarly located sclerites has been reported in many female elaterid beetles by Stein (1847), and Becker (1956). The latter author stated, however, that he was unaware that any particular function had been assigned to them. The presence of these sclerites was also illustrated by Hopkins (1915) for D. valens and the present author has found them in three of five other Dendroctonus species examined.

(iv) Accessory glands: Only one pair of accessory glands (AcGl) were found in the female beetle. These are located near the posterior end of the reproductive system and open laterally from the lower median region of the vagina. When filled they become greatly distended into an oval shape with the antero-ventral side elongated (fig. 24); when empty they become quite flat and inconspicuous (fig. 19).

There is no distinctive duct connecting from each gland to the vaginal pouch; the opening is loose and its periphery is lined with long spines (figs. 24A, 25; Spn). These spines project toward the gland interior. The cells lining the

accessory gland are dome shaped (fig. 24A, B, C; AcGlCl) and appear somewhat hexagonal externally. Each cell carries a short spine at its tip and all cells appear to be uniform in size except those adjacent to the opening, which possess larger spines and are similar to those surrounding the gland opening (fig. 25). In histological preparations the cell walls retained some rigidity and contained a shrunken mass of material within them. The cytoplasm at the base of each cell stained deeper than the shrunken material. A large oval-shaped nucleus is embedded within the cytoplasm of each cell. The gland is covered with a basement membrane which gives it a smooth appearance.

(v) Ovarioles and their histology: Each ovary of the mountain pine beetle consists of two ovarioles (figs. 19, 20), and this number is apparently consistent with all rhyncophorus beetles (Imms, 1957; Robertson, 1961). The ovariole is illustrated diagramatically in figure 26. It includes a short terminal filament (TlFil), a germarium (Germ), a vitellarium (Vit), and a posterior calyx (Clx) region. A sharp transition zone separates the germarium from the vitellarium. Within the vitellarium are the oocytes (Ooc) which are arranged singularly and increase in size from the transition zone posteriorly. Each developing oocyte with its surrounding tissue in the vitellarium constitutes an egg follicle (Fol). A thin epithelial sheath (EpSh) invests the entire ovariole.

The germarium is a lanceolate structure containing a dense

packing of germ cells from which the nutritive and oocyte cells become differentiated. In a newly developed female two sizes of nuclei were observed, the larger of the two were most numerous (fig. 28). For an egg-laying female on the other hand, only the larger nuclei were observed, even though the small cells may have been present. Moreover, the nuclei of the egg-laying female germarium were larger than the largest nuclei observed in the immature female, and because of this they presented a more densely packed appearance (figs. 27, 29, 30). In both females, however, there appeared to be little or no stratification of nuclei within the germarium; all nuclei appeared to be of uniform size and were evenly distributed. The larger nuclei are undoubtedly the trophocytes while the smaller may represent the precursors of the prefollicular epithelial cells found at the anterior end of the vitellarium (fig. 30; PreFolEpth). The trophocytes are more or less circular and appear to be uninucleate. In figure 28 the smaller nuclei are seen scattered singly throughout the germarium. Schlottman and Bonhag (1956) report an identical situation in <u>Tenebrio molitor</u> and apply the term "interstitial nuclei" to these scattered nuclei. They believe that the interstitial cells give rise to or contribute to the prefollicular tissue.

At the transition zone there is an abrupt change of microstructures (fig. 30). Here the young oocytes seem to separate from the germarium in fair abundance and are at first, very small. When first differentiated from the germarium they

appear to be embedded in a common cytoplasm. However, as they grow in size and move posteriorly the oocytes take up a median position in the vitellarium tube (fig. 31). At the same time they become surrounded by the prefollicular epithelial cells (figs. 30, 31). These cells are clearly visible first at the anterior end of the vitellarium where they are abundent. They appear as elongated cells arranged laterally from the walls of the vitellarium (fig. 30), and form a single layer of cells around each oocyte; this layer is known as the follicular epithelium (fig. 32; FolEpth).

Although no clearly distinctive cytoplasmic cords were observed extending from the germarium to the young oocytes, there was some indication that a cytoplasmic substance had moved into the vitellarium from the lateral margins of the transition zone (fig. 30). This material is probably a derivative of the nutritive cells and may constitute the major nutritive material of young oocytes, at least during the early stages of vitellogenesis.

The follicular epithelium surrounding each developing oocyte consists of a thick layer (fig. 31). As the young oocyte increases in volume the follicular cells become more flattened as in figure 32. Bonhag (1959) suggested that the follicular cells cope with the fast expanding area of a growing oocyte in two ways. The follicular cells may increase in number by mitosis, or they may become flatter by lateral stretching.

At the base of each ovary is a widened region known as

the calyx (fig. 19). Its inner lining is muscular and is convoluted (fig. 35; Mcl) when not functioning such as during ovulation. There did not appear to be a distinctive pedicel region, commonly found in most insect ovarioles.

The terminal filament extends from the anterior tip of the germarium and is separated from the germarium by a septum. The filament seems to function only for suspension. A thin epithelial sheath surrounds each entire ovariole and is continuous over the calyx region and the terminal filament (fig. 35; EpSh). The structure of this sheath consists of two layers of flat fibers, one layer orientated more or less at right angles with the second, giving a net-like appearance. An outer basement membrane provides a covering. Scattered among the fibers are numerous oval shaped nuclei. This sheath is capable of considerable expansion as observed during egg development. The histological studies did not reveal any tracheal branches deeper than the inside of the epithelial sheath. In addition to the outer epithelium, there was some evidence for the presence of an inner ovariole sheath or tunica propria.

(vi) Spermatheca: This organ is for sperm storage and it also controls the placement of spermatozoa for egg fertilization. It consists of a pump organ (SpthPm) provided with compressor muscles (CmpMcl) and a sac (SpthSa) (figs. 36, 37).

When the reproductive system is viewed dorsally the spermatheca is usually seen curved to the right of the median

oviduct (figs. 20, 22A). The pump organ is sclerotized and is easily recognized in the abdomen. It forms a U-shaped capsule and its sclerotization is necessary to provide the required springiness. As its tip is a small sclerotized projection to which the compressor muscle is fixed. This band of muscle connects to the basal portion of the capsule. By contraction and expansion it can effect the necessary pumping action to eject the spermatozoa. When viewed through the microscope the pump organ displays a sculptured pattern (fig. 36). However, in cross-section, this sculpturing is actually on the inner surface and shows up as a series of small ridges, particularly noticeable on the posterior half of the capsule (fig. 37). This extra sclerotization may be necessary to allow bending in the proper plane. A thin nucleated epithelial sheath (EpSh) surrounds the pump organ (fig. 37).

Leading posteriorly from the pump organ is the spermathecal duct, which passes medially between the copulatory pouch and the median oviduct (figs. 21A, 23, 24). It opens into the median egg tube at a point almost directly below the posterior end of the vagina (fig. 21A). In transverse sections the duct, for most of its length is circular, but upon entering between the muscle layers of the vagina and the median oviduct, it becomes flattened. A cross-section of the duct is shown in figure 23 and consists of cells arranged radially about the central passageway. An inner lining is also present. Since no muscle fibers were found on the duct wall this adds support

to the described function of the pump organ. In addition, it is possible to eject the sperm mechanically through the spermathecal duct by applying pressure on the pump organ with a pair of forceps.

The spermathecal sac joins the pump organ through a valve-like opening (figs. 33, 34, 37; SpthVl). The histological studies of the sac revealed it to be thick walled with many nuclei and spherical openings throughout (figs. 33, 37). This may suggest a glandular function.

Hopkins (1915) named the pump organ in D. valens the "spermatheca" and the sac portion the "spermathecal gland". Richmond's (1935) description for the mountain pine beetle spermatheca was consistent with Hopkins' except that he termed the pump organ the "spermathecal sac". However, in the present study it was appropriate to designate the pump organ and the sac as the spermatheca proper. This terminology is based on the fact that spermatozoa have never been found in the sac without also being present in the pump organ (figs. 33, 34, 37; Spz). Within the pump organ the spermatozoa appear to be oriented longtitudinally with respect to the capsule. The exact orientation of the sperm heads could not be determined, however, they seemed to point both towards and away from the spermathecal duct opening. The sperm in the sac occur in a random arrangement (fig. 37).

(vii) Egg Formation: Once a female beetle has entered the inner bark tissue of a host tree her feeding is concurrent with gallery excavation. During the first few days, rapid development of the ovaries ensues and egg-laying usually begins after three to four days of successful gallery construction. Egg-laying

usually continues until the beetle is disturbed by some environmental or physiological factor. For maximum development of the ovaries, several factors are undoubtedly necessary. Included among them are mating, favorable conditions of the host, and suitable environmental agencies (Reid, 1958b, 1961, 1962a, 1962b).

In a newly developed female the ovaries appear as in figure 19. At this time seven to nine immature oocytes can be distinguished within the vitellarium. As feeding commences, all oocytes begin to enlarge, and at the same time differentiation of young oocytes from the germarium takes place. The ovarioles soon become distended and may appear as in figure 26 when at maximum egg production, but in a compact configuration as in figure 32. The oocytes first differentiated are small and have prominent nuclei. However, enlargement follows rapidly, with an increase in both cytoplasmic and nuclear substances. Within the younger egg nuclei, conspicuous nucleolar bodies occur regularly and appear to be strongly acidophilic. Several similar but smaller stained bodies also were present in the nucleus. The latter may be homologous with the "emission bodies" recorded by Schlottman and Bonhag (1956).

The nuclei of most of the immature oocytes maintained a near central position and stained lighter than the surrounding cytoplasm (figs. 31, 32). As the egg neared maturity, however, the nucleus could be found, in many cases, in a lateral position, and at such times was less conspicuous. Bonhag (1958, 1959)

reported a similar phenomenon in the ovaries of the milkweed bug and American cockroach. A median position is demonstrated in figure 35, although this may be a rare event.

Once the developing oocyte reaches a certain size, the deposition of yolk (Ylk) takes place and is distinguished from the deeply stained cytoplasm by numerous spherical bodies figs. 32, 35). Much of this yolk material is believed to be mediated through the follicular epithelial cells (Schlottman and Bonhag, 1956; Bonhag, 1958, 1959). According to these authors the egg nucleus undergoes a gradual transformation during oocyte enlargement. During this period the nucleus appears to serve a special function when yolk accumulation takes place and it has been termed a "germinal vesicle". This term may also be applicable to the egg nucleus of the mountain pine beetle. The changes that occur during nucleus transformation are complicated, however, and the exact function of the germinal vesicle is still obscure.

It was stated earlier that a follicular epithelium completely surrounds each yolk-filled oocyte until the time of its release during ovulation. The follicular epithelial cells in the anterior half of the ovariole form a thick layer and their cell boundaries are indistinct. Each follicle cell is uninucleate (fig. 35); this is characteristic for all follicular cells of the vitellarium. Usually, the epithelial cell boundaries of the last one or two follicles become distinct as the cells become squamous. In the most posterior follicle egg

enlargement reaches a maximum and is followed by the secretion of the chorion, a product of the follicular cells of that follicle. The chorion forms an outer investment of each egg and its formation marks the completion of a developing oocyte.

Following the secretion of the chorion, the cells of the last follicle break down and their nuclei are often recognized with difficulty (fig. 35). The mature egg is now ready for ovulation. Each egg is oval shaped and measures about one millimeter in length. The outer surface of the chorion is finely sculptured.

In the cockroach ovariole, Bonhag (1959) listed three known functions of the follicular epithelium and they may all be applicable to the mountain pine beetle. Thus the epithelium may, (1) act as a mediator for chemical substances passing from the blood to the oocyte, serving a trophic function, (2) secrete the chorion when the egg has reached maturity, and (3) resorb yolk material whenever completion of egg development fails to take place.

(viii) Ovulation: The pathway which the mature oocyte follows during ovulation begins as shown in figure 35. At the base of the vitellarium and extending a short distance into the calyx region is the so-called epithelial plug (EpPlg). It appears to be composed of the degenerative follicular epithelial cells of the last egg follicle. An accumulation of this cellular mass occurs after each ovulation and numerous follicular cell nuclei can be recognized within it (fig. 35). Soon after each

ovulation the follicular cells which compose the epithelial plug undergo autolysis (Wigglesworth, 1953; Schlottman and Bonhag, 1956) so that the cell boundaries become indistinct. At this stage the cellular mass turns a bright yellow coloration, and as such it is recognized as the corpus luteum (fig. 35; Clt). Some of this material may be reabsorbed by the calyx epithelium, but there is evidence that some may also be discharged out through the egg tube in front of an ovulating egg.

At the time of ovulation the mature oocyte ruptures the epithelial plug or corpus luteum and enters into the oviduct system. The oviduct stretches to about three times its normal diameter with the presence of an egg. The oocyte then moves posteriorly by the peristaltic activity of the oviduct muscles. In conjunction with peristalsis, the chitinous intima of spines in the oviduct may be an important aid for the posterior movement of the egg. This seems especially true for the posterior end of the egg tube where greater resistance is met with the dorsal copulatory pouch and thicker muscle tissue surrounding the terminal portion of the oviduct (fig. 21A).

Fertilization is believed to take place when the egg approaches the posterior opening. Hence the contraction of the spermathecal pump to provide spermatozoa, must be synchronized with the passage of the egg at the opening of the spermathecal duct (fig. 21A). The egg is then ejected from the abdomen through the genital opening and deposited in a

specially constructed niche on the lateral margin of the egg gallery (Reid, 1958b).

According to Reid (1958b), the egg niche is excavated always at the anterior end of the beetle's gallery. After this the female must back down the gallery to a point where she can turn around and then proceed backwards toward the excavated niche. These events signify a certain warning period for ovulation which may be triggered by the rupturing of the epithelial plug. However, the exact mechanism of ovulation in insects is not understood (Wigglesworth, 1953).

A few females were removed from their egg galleries at such time when they displayed a behavior corresponding to one of the egg-laying events described above. Of five such females examined, four contained mature oocytes, one each, within the median oviduct and all showed well developed ovaries. This evidence may suggest that the stimulus to construct an egg niche is received well in advance of egg deposition and that it takes a few minutes for the mature oocyte to pass from the last follicle into the calyx region.

The normal passage taken by the oocyte during ovulation is apparently from the posterior end of the median oviduct, thence through the genital opening (fig. 21A). There were many occasions, however, when instead of passing to the exterior, the egg was passed dorsally into the vaginal region and then to the bursa copulatrix. The morphological features described for this dorsal diverticulum suggest that once within this

pouch that the egg cannot be released in normal condition. To begin with, the dorsal rows of spines within the vagina, in combination with the musculature of that region probably have a destructive effect and are orientated to restrict posterior movement. Furthermore, the spiny plates of the bursa copulatrix plus its strong musculature and basal constriction all appear to point to an inevitable fate of the oocyte. The spiny sclerites are probably responsible for the rupturing of the chorion since they can operate with a rasping action. Finally, the appearance of egg membranes, yolk, remnants of spermatophores, and spermatozoa was of common occurrence in the female accessory glands and it is a combination of this material which accounts for much of their increased volume. The elongated spines surrounding the accessory gland opening probably do justice in keeping the contents within and may help in its maceration. On occasions as many as seven distinctive chorion membranes have been extracted from both glands. In another instance six spermatophores were found in the female reproductive system, one in the vagina, four in one accessory gland, and one in the opposite gland. This occurred when a few females were stored with fresh bark chips and with a greater proportion of males.

Previous workers have termed the female accessory glands "colleterial" (Richmond, 1935; Reid, 1958a). However, the histological findings cited above do not support a colleterial function for these glands in D. monticolae. Instead, the

accessory glands appear to operate in conserving valuable nutrient material and thus may function in a reabsorbing capacity.

No complete explanation can be given for the dorsal passage of the mature oocyte, rather than via the normal posterior route. In observation plates where the bark tissue was allowed to dry rapidly after a female had reached the egg-laying stage, it was observed that her accessory glands invariably contained a yolk-like substance and chorion membranes as well. This material appeared to accumulate at variable rates and was often in one gland more than in the other. Furthermore, if the female was left for several days before examination, much of the accessory gland contents transformed to a yellow oily liquid which usually separated from the rest of the gland material. This condition appeared regularly in egg-laying females taken from infested logs. When dissected in water or physiological saline the yellow fluid was immiscible with these solutions and floated over the surface. The presence of this yellow material may suggest that autolysis has taken place.

Rapid drying of the host tissue may be one of several means by which egg production is abruptly halted. According to Reid (1962b), if an egg producing female is disturbed by an abnormal change of environmental factors, she usually responds by ceasing feeding and gallery construction. If this occurs when fully matured oocytes are present in the vitellarium, these eggs may be involuntarily discharged into the oviduct

system. Since there are no egg niches present for deposition the normal pattern of activity is interrupted, hence the egg is kept internal. Another possible explanation may result from disturbance by the male. It was observed in the observation plates that the male often interferred with the female when she was backing up during an egg-laying period. Any such delay in egg deposition might conceivably lead to the dorsal movement of the egg into the copulatory chamber.

(ix) Changes in female reproductive organs: Reid (1962b) described the general conditions of the ovaries and spermatheca and noted the presence of corpora lutea in female adults throughout their life cycle. The present morphological study reveals no major changes except at the cellular level. A comparison between the nuclei of a newly developed female germarium and for an egg-laying female has already been mentioned. Although most ovaries of the overwintering females showed much reduction, the accessory glands were usually filled as in figure 20. Nine such females examined showed enlarged accessory glands and all glands displayed a yellow coloration.

(d) MATING PROCESS

The mating behavior of the mountain pine beetle was adequately described and illustrated by Reid (1958b). To add to his description the following internal details were observed and may explain the behavior pattern during mating.

While mating the male is usually upside down relative to

the female (fig. 1). This position seems necessary when one considers the internal structure of the copulatory pouch and the position of the male gonopore (fig. 14). Measurements of the male and female genitalia reveal that the male intromittent organ does not extend into the bursa copulatrix during coitus; the posterior tip of the internal sac extends only to the bursa sclerites. Furthermore, it appeared that the sac is fully everted only when within the female vagina. Figure 24A shows the vaginal pouch with a median depression into which the median lobe of the male internal sac fits, the lateral lobes project laterally and thus secure a fixed position until the male secretion product has been deposited. When in the upside down position the dorsally located male gonopore can then eject the spermatophore ventrally in the female, depositing it in the median groove of the vagina. This position is in close contact with the spermathecal duct opening to which the spermatozoa migrate. An examination of females immediately following mating revealed the spermatophore in the position described.

When the mating process was observed under magnification a series of wave-like motions could be detected through the connecting membrane of the male genital organ. These motions were probably a result of the contraction of the ejaculatory duct. In one observed mating which lasted for about one minute, more than 20 such contractions were recorded. During each contraction seminal fluid is ejected posteriorly, the sum total

of which is deposited as a single mass for which the term spermatophore has been used.

From the vagina the spermatophore may enter the bursa copulatrix where it has often been found. Williams (1945) recorded the presence of a pair of chitinous plates on the walls of the bursa copulatrix in two elaterid species. He suggested that these may be used to rupture the spermatophore. The bursa sclerites of the mountain pine beetle may function similarly. Following the release of spermatozoa it appears that the spermatophore is ultimately forced into one of the accessory glands.

No attempt was made to determine the period of time required for the spermatozoa to reach the spermatheca but it is believed to be a matter of a few minutes. Francke-Grosmann (1950) suggested that in D. micans the pump organ may act both ways, ie., the spermatheca is filled and emptied by pumping. Perhaps the musculature of the median oviduct and vagina, which surrounds much of the spermathecal duct, aid the movement of spermatozoa into the spermatheca.

DISCUSSION

In the evolution of the reproductive organs of the mountain pine beetle there appears to have been a trend toward both specialization and simplification. In male beetles the features which are indicative of simplification are the complete lack of external accessory structures of an appendicular nature,

a probable reduction in the number of testicular follicles, and the reduced vasa efferentia. The spermatophore appears to be a simplified type.

In general, the genital organ and its accessory sclerites and complicated musculature are suggestive of specializations. The funnel mechanism and accessory gland arrangement may be peculiar to several genera of bark beetles. Finally, the position described for mating is identical with the position observed for D. micans (Francke-Grosmann, 1950) and may be a special modification for gallery constructors.

For the female beetle a loss of all accessory sclerotizations of the posterior abdomen and a reduction in the number of ovarioles are simplifications. The structure of the bursa copulatrix and its sclerites when considered in view of their functions, may be a modification toward specialization. Furthermore, at least part of the functions of the bursa copulatrix are closely allied with the peculiarities observed in the accessory glands. The gland structures may also have undergone specialization since no analogous situation for other insects was found in the literature. However, few intensive studies of both male and female accessory glands have been undertaken.

Several authors including Krause (1946), Bryan (1954), and Schlottman and Bonhag (1956) have described Polyphagan ovarioles and all were found to be telotrophic. The work of Schlottman and Bonhag is especially significant since they pointed out many of the differences between the typical telotrophic ovariole of a hemipteran insect and a telotrophic beetle

(Tenebrio molitor). In addition, the histological structure of the mountain pine beetle ovariole shares many similarities with the condition observed in T. molitor and in Popilius disjunctus Illiger and Macrodactylus subspinosus (Fab.) by Bryan (1954). Although typical nutritive cords were not observed in D. monticolae it is quite definite that the apical cells of the germarium are trophocytes rather than oogonia. According to Bonhag (1958) this is the criterion used to distinguish the telotrophic ovariole from the panoistic type. It is fairly clear that the bark beetle ovary is telotrophic or a modification of that type. Bonhag also pointed out that the nutritive cords of the Polyphagan telotrophic ovariole are generally inconspicuous and may even be missing in some species.

The term colleterial gland has been widely used by many workers (Hopkins, 1915; Schedl, 1931; Richmond, 1935; Chapman, 1958; and others) to designate the female accessory glands in bark beetles. However, this terminology does not appear justified, and since these glands are common in bark beetles they may well function as described for the mountain pine beetle.

The studies of the female reproductive system and the behavior of the adult female during egg-laying and gallery construction revealed several characteristics in which fecundity may be strongly influenced. To begin with a small and variable number of eggs is laid, with an average of 75 eggs per egg gallery (Reid 1962b). Secondly, egg-laying is often spread over a lengthy period with each egg laid singly and more or less at specified intervals along the gallery. It was earlier noted that the egg-laying

female is easily interrupted and a rapid decline in oviposition follows. Robertson (1961) has suggested that the small number of ovarioles may indicate a low reproductive potential which in turn may reflect a somewhat sheltered existence and easy access to food for bark beetles generally. In addition, many fully matured oocytes never reach the exterior of the abdomen but are ultimately autolyzed in the accessory glands.

SUMMARY

1. The male reproductive system consists of the following structures: There are two testes, each with six follicles and two vasa efferentia. A vas deferens which functions partly as a seminal vesicle, extends from each testis to the accessory gland region. Two pairs of accessory glands are described and good evidence exists for a third pair. All glands feed into the ejaculatory duct at the same point. The median ejaculatory duct fastens posteriorly onto the internal structure of the genital organ. This accessory structure and a spicule, tegmen, internal sac and other associated membranes and musculature form an integral part of the complicated copulatory organ.

2. The operation of internal sac eversion is outlined on the basis of the muscles and their attachments on the

copulatory organ. When fully everted the internal sac consists of two lateral lobes and a larger median lobe; all are membranous and each carries an armature of spicules. A capsule-like structure at the tip of the median lobe is believed to be sensory and perhaps also glandular in function.

3. The female organs of reproduction consist of two ovaries, each with a pair of telotrophic ovarioles, a pair of short lateral oviducts, a longer median oviduct, a dorsal copulatory pouch consisting of vagina and bursa copulatrix, a pair of accessory glands, and a spermatheca.

4. Each ovariole has a terminal filament for suspension, an outer epithelial sheath covering, and is divided into three zones; germarium, vitellarium, and calyx. The germarium contains two sizes of densely packed nuclei; the larger ones are most numerous and are probably trophocytes. The smaller nuclei may be the precursors for the prefollicular epithelium. A sharp transition zone divides the germarium from the vitellarium; the latter contains the developing oocytes surrounded by follicular epithelium. Each oocyte with its layer of follicular cells is an egg follicle, and in the last and largest follicle of the vitellarium, a chorion membrane is secreted by the follicular epithelial cells. An epithelial plug or corpus luteum separates the vitellarium from the muscular calyx.

5. The oviducts, vagina, and bursa copulatrix are all muscular tubes. A pair of sac-like accessory glands open

laterally into the vagina. Short spines occur on the inner lining of the median oviduct, the inner dorsal lining of the vagina, and larger spines surround the opening into the accessory gland. Two spiny sclerites are also present on the inner lining of the basal bursa copulatrix.

6. The spermatheca opens into the posterior end of the median oviduct and consists of a pump organ and a sac. The pump and sac store the spermatozoa and constitute the spermatheca proper. A glandular function has also been suggested for the spermathecal sac. The pump organ is connected to the median oviduct by a short non-muscular duct.

7. Evidence is provided that suggests a reabsorbing function for the female accessory glands. Egg contents, sperm, and spermatophores have been found in these glands where autolysis appears to take place. In addition, the bursa copulatrix and its sclerites seem to function partly in conjunction with the accessory glands.

8. During mating a spermatophore is deposited in the female vagina and consists of spermatozoa plus secretions from at least two of the paired male accessory glands.

REFERENCES

Anderson, J.M., 1950. A cytological and cytochemical study of the male accessory gland in the Japanese beetle, Popillia japonica Newman. Biol. Bull., Wood's Hole 49: 49-64.

Atkins, M.D. and J.A. Chapman, 1957. Studies on nervous system anatomy of the Douglas fir beetle, Dendroctonus pseudotsugae Hopk. (Scolytidae). Canad. Ent. 89 : 80-86.

Atkins, M.D. and S.H. Farris, 1961. A contribution to the knowledge of flight muscle changes in the Scolytidae (Coleoptera). Canad. Ent. 94 : 25-32.

Becker, E.C., 1956. Revision of the Nearctic species of Agrotes (Coleoptera : Elateridae). Canad. Ent. 88, Suppl. 1, pp. 1-101.

Bissel, T.L., 1937. Structure of the reproductive system of the pecan weevil (Cutculionidae). Ann. ent. Soc. Amer. 30 : 242-251.

Blunck, H., 1912. Das Geschlechtsleben des Dytiscus marginatus Lec. Z. wiss. Zool. 102 : 12-248.

Bonhag, P.F., 1958. Ovarian structure and vitellogenesis in insects. Annual Rev. Ent. 3 : 137-160.

Bonhag, P.F., 1959. Histological and histochemical studies on the ovary of the American cockroach, Periplaneta americana (L.). Univ. Calif. Publ. ent. 16 : 81-124.

Bonhag, P.F. and W.J. Arnold, 1961. Histology, histochemistry, and tracheation of the ovariole sheaths in the American cockroach, Periplaneta americana (L). J. Morph. 108 : 107-129.

Bonhag, P.F. and J.R. Wick, 1953. The functional anatomy of the male and female reproductive systems of the milkweed bug, Oncopeltus fasciatus (Dallas) (Heteroptera : Lygaeidae), J. Morph. 93 : 177-284.

Bruhn, A.F., 1947. The external male genitalia of some Rhyncophora. Gr. Basin Nat. 8 : 1-35.

Bryan, J.H.D., 1954. Cytological and cytochemical studies of oogenesis of Popilius disjunctus Illiger (Coleoptera - Polyphaga). Biol. Bull., Wood's Hole 107 : 64-79.

Burke, H.R., 1959. Morphology of the reproductive systems of the cotton boll weevil (Coleoptera, Curculionidae). Ann. ent. Soc. Amer. 52 : 287-294.

Chamberlin, W.J., 1939. The bark and timber beetles of North America north of Mexico. OSC Co-operative Association, Corvallis, Oregon, 513 pp.

Chamberlin, W.J., 1958. The Scolytoidea of the Northwest: Oregon, Washington, Idaho, and British Columbia. OSC Monographs, Studies in Entomology 2, OSC Press, Corvallis, Oregon, 205 pp.

Chapman, J.A., 1956. Physiological and biological studies on the ambrosia beetle, Trypodendron lineatum (Oliv.). Interim Report 1955-2, Forest Biology Laboratory, Victoria, B.C.

Chapman, J.A., 1958. Studies on the physiology of the ambrosia beetle Trypodendron in relation to its ecology. Proc. Xth. int. Congr. Ent. 4 : 375-380.

Crampton, G.C., 1929. The terminal abdominal structures of female insects compared throughout the orders from the standpoint of phylogeny. J. New York ent. Soc. 37 : 453 - 512.

Cros, A., 1924. Emission d'un spermatophore par divers Coléoptères. Bull. Soc. Sci. Nat. Maroc 4 : 98-103.

Crowson, R.A., 1960. The phylogeny of Coleoptera. Annual Rev. Ent. 5 : 111-134.

Davenport, H.A., 1960. Histological and histochemical Technics. W.B. Saunders Co. London. xxii + 401 pp.

Davey, K.G., 1958. The migration of spermatozoa in the female of Rhodnius prolixus Stal. J. exp. Biol. 35 : 694-701.

Davey, K.G., 1960. Evolution of spermatophores in insects. Proc. R. ent. Soc. Lond. (A) 35 : 107-113.

Davis, N.T., 1956. The morphology and functional anatomy of the male and female reproductive systems of Cimex lectularius L. (Heteroptera, Cimicidae). Ann. ent. Soc. Amer. 49 : 466-493.

Deegener, P., 1928. Geschlechtsorgane. In : Schröder's Handbuch der Entomologie. 1, Fisher, Jena. pp. 466-518.

De Leon, D., W.D. Bedard, and T.T. Terrell, 1934. Recent discoveries concerning the biology of the mountain pine beetle and their effect on control in western white pine stands. J. For. 32 : 430-436.

Escherich, K., 1894. Anatomische Studien über das männliche Genitalsystem der Coleopteren. Z. wiss. Zool. 57 : 620 - 641.

Evenden, J.C., W.D. Bedard, and G.R. Struble, 1943. The mountain pine beetle, an important enemy of western pines. U.S.D.A. Circ. No. 664.

Fisher, T.W., 1959. Occurrence of spermatophores in certain species of Chilocorus (Coleoptera : Coccinellidae). Pan-Pacif. Ent. 35 : 205-208.

Francke-Grosmann, H., 1948. Über den Kopulationsapparat ~~des~~ des Riesenbastkafers, Dendroctonus micans Kug. Verh. dtsch. Zool., Kiel, pp. 219-225.

Francke-Grosmann, H., 1950. Über Kopulation, Eiablage and Gelbkörperbildung beim Riesenbastkafer Dendroctonus micans Kug. Verh. dtsch. Ges. angew. Ent., München, 1949. Verl. parey. pp. 142-153.

Friedmann, N., 1934. Ein Beitrag zur Kenntnis der embryonalen Entwicklung der Abdominalfüsse bei den Schmetterlingsraupen. Soc. Sci. Fennica, Commentationes Biol. 4 : 1-29.

Gustafson, J.F., 1950. The origin and evolution of the genitalia of the Insecta. Microentomology 15 : 35-67.

Hay, J.C., 1956. Experimental crossing of mountain pine beetle with Black Hills beetle. Ann. ent. Soc. Amer. 49 : 567-571.

Heberdey, R.F., 1931. Zur Entwicklungsgeschichte, vergleichenden Anatomie und Physiologie der weiblichen Geschlechtsausführwege der Insekten. Z. Morph. Okol. Tiere 22 : 416-586.

Hodson, A.C., 1934. The origin and differentiation of the sex organs of Tribolium destructor Duval Ann. ent. Soc. Amer. 27 : 278-291.

Hopkins, A.D., 1909. Contributions towards a monograph of the scolytid beetles. I. The genus Dendroctonus. U.S.D.A. Bur. Ent. Tech. Ser. No. 17 : 67 pp.

Hopkins, A.D., 1911. Contributions towards a monograph of the barkweevils of the genus Pissodes. U.S.D.A. Tech. Ser. 20 : 1-68.

Hopkins, A.D., 1915. Preliminary classification of the superfamily Scolytoidea. U.S.D.A. Bur. Ent. Tech. Ser. No. 17 : 165-232.

Hopping, G.R., 1946. Control of the more injurious bark beetles of the Canadian Rocky Mountain region. Can. Dept. Agr., Div. Ent., Proc. Pub. No. 49.

Imms, A.D., 1957. A general Textbook of Entomology. Methuen and Co., Ltd., London. x + 886 pp.

Jackson, D.J., 1960. Observations on egg-laying in Ilybius fuliginosus Fabricius and I. ater Degeer (Coleoptera : Dytiscidae), with an account of the female genitalia. Trans. R. ent. Soc. Lond. 112 : 37-52.

Khalifa, A., 1949. Spermatophore production in Trichoptera and some other insects. Trans. R. ent. Soc. Lond. 100 : 449-479.

Krause, J.B., 1946. The structure of the gonads of the woodeating beetle, Passalus cornutus Fab. Ann. ent. Soc. Amer. 39 : 193-206.

Lindroth, C.H.and E. Palmén, 1956. Coleoptera. In : Taxonomist's glossary of genitalia in insects, ed. by S.L. Tuxen, Munksgaard, Copenhagen, pp. 69-76.

Matsuda, R., 1958. On the origin of the external genitalia of insects. Ann. ent. Soc. Amer. 51 : 84-94.

Metcalfe, M.E., 1932. The structure and development of the reproductive system in the Coleoptera with notes on its homologies. Quart. J. micr. Sci. 75 : 49-130.

Michener, C.D., 1944. A comparative study of the appendages of the eighth and ninth abdominal segments of insects. Ann. ent. Soc. Amer. 37 : 336-351.

Muir, F., 1918. Notes on the ontogeny and morphology of the male genital tube in Coleoptera. Trans. R. ent. Soc. Lond.: 223-229.

Muir, F., 1920. On the mechanism of the male genital tube in Coleoptera. Trans. R. ent. Soc. Lond. (1919) : 404-414.

Munro, J.W., 1914. Notes on the reproductive organs of the pine weevil (Hylobius abietis). Proc. R. phys. Soc. Edinb. 19 : 161-169.

Nüsslin, O., 1911. Phylogenie und System der Borkenkäfer. Z. wiss. InsektBiol. Bd. 7, No. 1-12.

Nüsslin, O., 1912. Phylogenie und System der Borkenkäfer. Z. wiss. InsektBiol. Bd. 8, No. 1-7.

Pantin, C.F.A., 1960. Notes on microscopical technique for zoologists. Cambridge, University Press. viii + 77 pp.

Reid, R.W., 1958a. Internal changes in the female mountain pine beetle, Dendroctonus monticolae Hopk., associated with egg laying and flight. Canad. Ent. 90 : 464-468.

Reid, R.W., 1958b. The behavior of the mountain pine beetle, Dendroctonus monticolae Hopk., during mating, egg laying, and gallery construction. Canad. Ent. 90 : 505-509.

Reid, R.W., 1961. Moisture changes in lodgepole pine before and after attack by the mountain pine beetle. For. Chron. 37 : 368-376.

Reid, R.W. 1962a. Biology of the mountain pine beetle, Dendroctonus monticolae Hopkins, in the East Kootenay region of British Columbia. I. Life cycle, brood development, and flight periods. Canad. Ent. 94 : 531-538.

Reid, R.W., 1962b. Biology of the mountain pine beetle, Dendroctonus monticolae Hopkins, in the East Kootenay region of British Columbia. II. Behavior in the host, fecundity, and internal changes in the female. Canad. Ent. 94 : 605-612.

Richmond, H.A., 1935. A morphological study of the bark beetle Dendroctonus monticolae Hopk. Unpub. thesis, Faculty of Graduate Studies, Mcgill University, Montreal.

Robertson, J.G., 1961. Ovariole numbers in Coleoptera. Can. J. Zool. 39 : 245-263.

Ryan, R.B., 1959. Termination of diapause in the Douglas fir beetle, Dendroctonus pseudotsugae Hopk. (Coleoptera : Scolytidae), as an aid to continuous rearing. Canad. Ent. 91 : 520-525.

Schedl, K.E., 1931. Morphology of the bark beetles of the genus Gnathotrichus Eichh. Smithson. misc. Coll. 82 : 1-88.

Schlottman, L.L. and P.F. Bonhag, 1956. Histology of the ovary of the adult mealworm Tenebrio molitor L. (Coleoptera, Tenebrionidae). Univ. Calif. Publ. ent. 11 : 351-394.

Scudder, G.G.E., 1961a. The comparative morphology of the insect ovipositor. Trans. R. ent. Soc. Lond. 113 : 25-40.

Scudder, G.G.E., 1961b. The functional morphology and interpretation of the insect ovipositor. Canad. Ent. 94 : 267-272.

Sharp, D., 1918. Studies in Ryncophora. IV. A preliminary note on the male genitalia. Trans. R.ent. Soc. Lond. 66 : 209-222.

Sharp, D.and F. Muir, 1912. The comparative anatomy of the male genital tube in Coleoptera. Trans. R. ent. Soc. Lond. 1912 : 477-642.

Shepherd, R.F., 1960-61. Personal communications.

Shteinberg, D.M., 1960. Adaptive features in the structure of female gonads in insects. A translation from Entomological Rev. 38 : 476-483.

Singh Pruthi, H., 1924a. On the post-embryonic development and homologies of the male genital organs of Tenibrio molitor L. (Coleoptera). Proc. zool. Soc. Lond. pp. 857-868.

Singh Pruthi, H., 1924b. On the development of the ovipositor and the efferent genital ducts of Tenibrio molitor L. (Coleoptera), with remarks on comparison of the latter organs in the two sexes. Proc. zool. Soc. Lond. pp. 869-883.

Snodgrass, R.E., 1931. Morphology of the insect abdomen. Part 1. General structure of the abdomen and its appendages. Smithson. misc. Coll. 85 : 1-128.

Snodgrass, R.E., 1933. Morphology of the insect abdomen. Part 11. The genital ducts and the ovipositor. Smithson. misc. Coll. 89 : 1-148.

Snodgrass, R.E., 1935. Principles of Insect Morphology. McGraw - Hill, New York. ix + 667 pp.

Snodgrass, R.E., 1936. Morphology of the insect abdomen. Part 111. The male genitalia (including Arthropods other than insects). Smithson. misc. Coll. 95 : 1-96.

Snodgrass, R.E., 1957. A revised interpretation of the external reproductive organs of male insects. Smithson. misc. Coll. 135 : 1-60.

Stein, F., 1847. Vergleichende Anatomie und Physiologie der Insekten. 1. Die weiblichen Geschlechtsorgane der Käfer. Duncker und Humblot, Berlin. 139 pp., 9 plates.

Swaine, J.M., 1918. Canadian bark beetles. 11. A preliminary classification with an account of the habits, injuries, and means of control. Can. Dept. Agr. Tech. Bull. No. 14.

Tanner, V.M., 1927. A preliminary study of the genitalia of female Coleoptera. Trans. Amer. ent. Soc. 53 : 5-50.

Verhoeff, K.W., 1893. Vergleichende Untersuchungen über die Abdominalsegmente und die Copulationorgane der männlichen Coleoptera. Dtsch. ent. Z., 1893 : 113-170.

Wigglesworth, V.B., 1953. The Principles of Insect Physiology. Methuen and Co., Ltd., London. viii + 546 pp.

Williams, J.L., 1945. The anatomy of the internal genitalia of some Coleoptera. Proc. ent. Soc. Wash. 47 : 73-87.

Wood, S.L., 1952. Observations on the homologies of the copulatory apparatus in male Coleoptera. Ann. ent. Soc. Amer. 45 : 613-617.

Zacharuk, R.Y., 1958a. Structures and functions of the reproductive systems of the prairie grain wireworm, Ctenicera aeripennis destructor (Brown) (Coleoptera : Elateridae). Canad. J. Zool. 36 : 725-751.

Zacharuk, R.Y., 1958b. Postembryonic development of the reproductive systems of the prairie grain wireworm, Ctenicera aeripennis destructor (Brown) (Coleoptera : Elateridae). Canad. J. Zool. 36 : 753-777.

PLATES

PLATE 1

Fig. 1. Lateral view of the abdomen and metathorax of a male and female beetle showing the typical mating position and the general location of the reproductive organs within the body cavity. Abd, Abdomen; AcGl, Accessory Gland; Metath, Metathorax; Ov, Ovaries; Preph, Prephragma; S, Sternum; SusLig, Suspensory Ligament; T, Tergum; Tes, Testis.

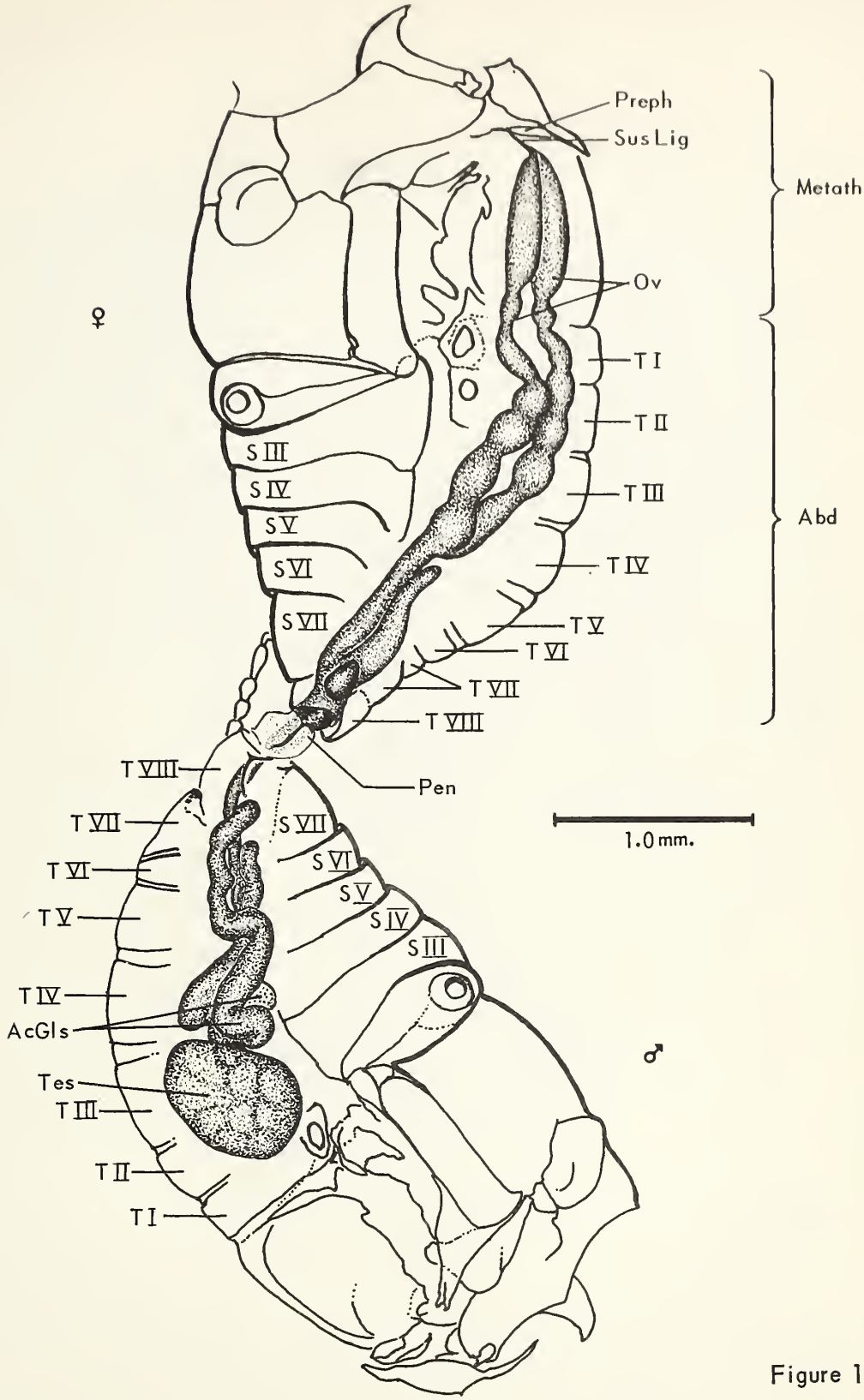

Preph
Sus Lig
Metath
Ov
♀
T I
T II
S III
S IV
S V
S VI
S VII
T III
Abd
T IV
T V
T VI
T VII
T VIII
Pen
T VIII
T VII
T VI
T V
T IV
AcGls
Tes
T III
T II
T I
S VII
S VI
S V
S IV
S III
1.0 mm.
♂

Figure 1

PLATE 2

Fig. 2. Ventral view of the male reproductive system showing the usual resting position of the copulatory organ and posterior attachments. The testes and accessory glands have been spread out somewhat. Abd, Abdomen; AcGl(a), Accessory Gland(a); AcGl(b), Accessory Gland (b); Anus; Apod, Apodeme; EjD, Ejaculatory Duct; GenOp, Genital Opening; Mcl, Muscle; Pen, Penis; S, Sternum; SmlD, Seminal Duct; Smlv, Seminal Vesicle; Spcl, Spicule; T, Tergum; Tes, Testes; Tgm, Tegmen; Vd, Vas deferens.

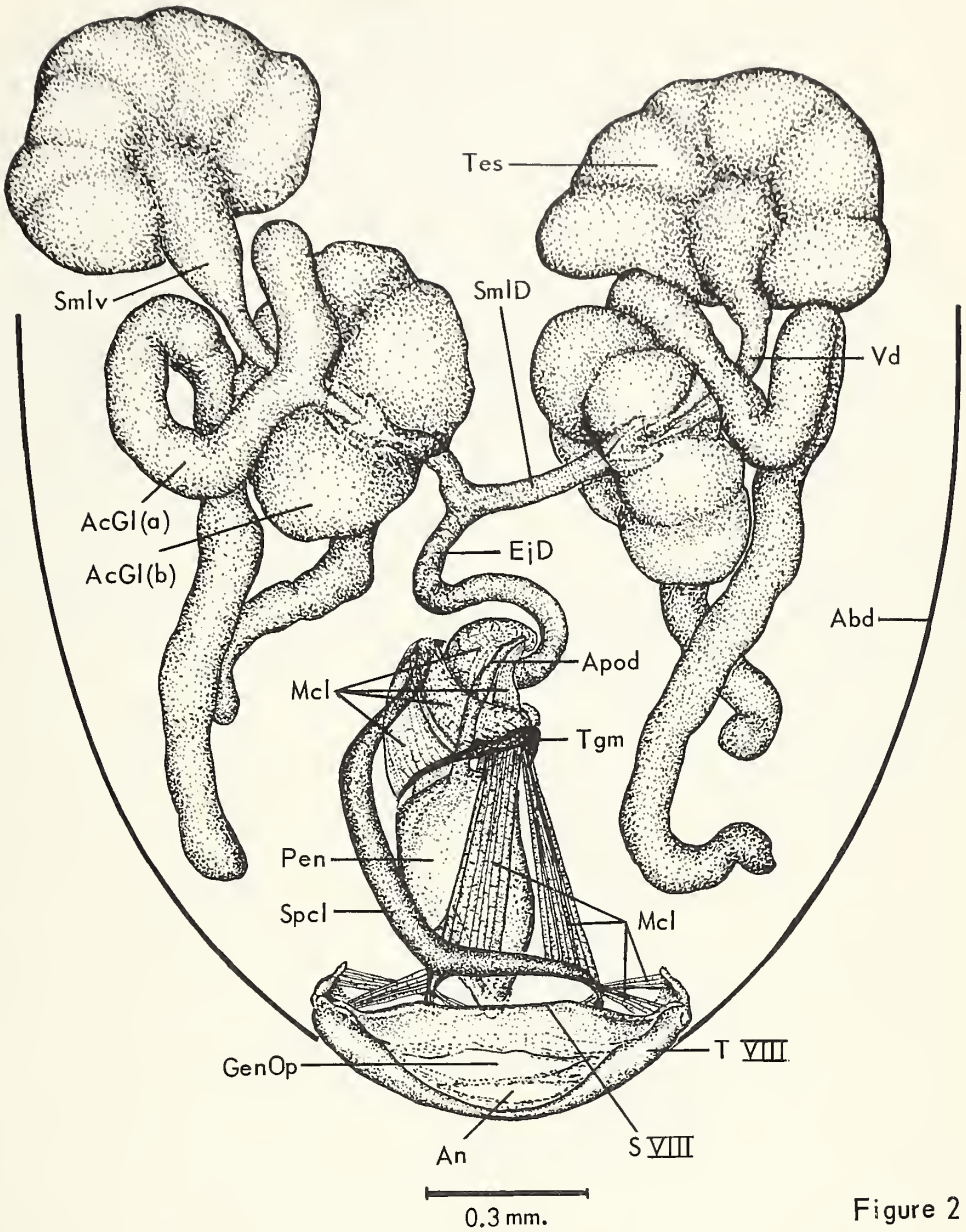

Tes
SmlD
Smlv
Vd
AcGl(a)
AcGl(b)
EjD
Abd
Apod
Mcl
Tgm
Pen
Spcl
Mcl
T VIII
GenOp
S VIII
An
0.3 mm.

Figure 2

PLATE 3

Fig. 3. Longtitudinal section through a testis showing distribution of germ cells, the follicles, and associated ducts. CytoPr, Cytoplasmic Process; EpSh, Epithelial Sheath; Fol, Follicle; Nuc, Nucleus; Sep, Septum; Smlv, Seminal vesicle; SpCst, Sperm Cyst; Spz, Spermatozoa; Vd, Vas deferens; Ve, Vas efferens.

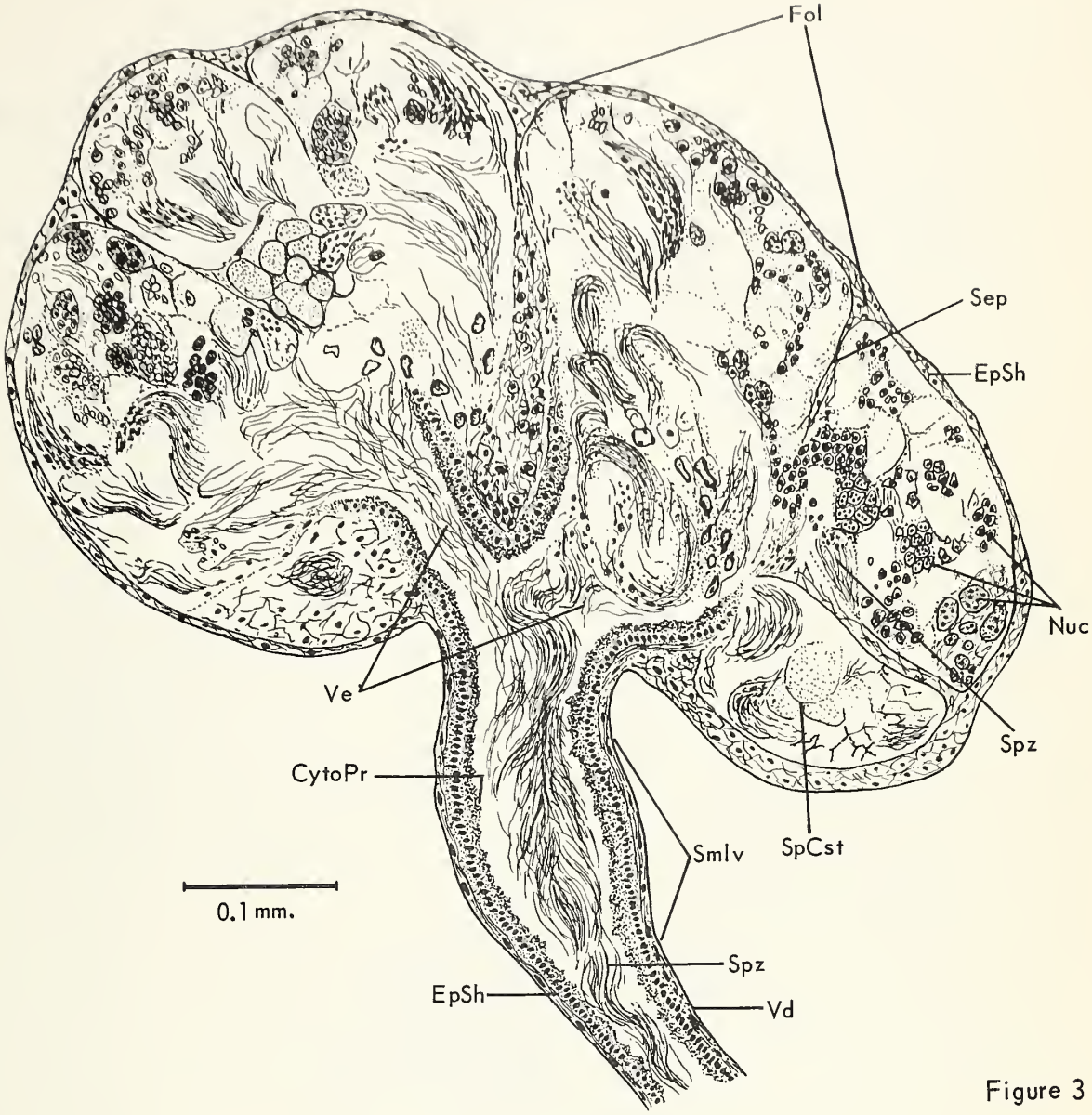


Figure 3

PLATE 4

Fig. 4. Longtitudinal view of all accessory glands and associated ducts of the male reproductive system. AcGl(b) and the funnel mechanism are represented diagramatically. The plane of view for figs. 5, 8, 9, and 10 is indicated. AcGl(a), Accessory Gland (a); AcGl(a)Fl, Accessory Gland (a) Fluid; AcGl(b), Accessory Gland (b); Fun, Funnel; Smld, Seminal Duct; Smlv, Seminal vesicle; Vd, Vas deferens; X, Unknown structure.

Fig. 5. Transverse section through the duct of AcGl(a), the vas deferens, and through X-structure, showing cellular structures and contents. AcGl(a)D, Accessory Gland (a) Duct; AcGl(a)Fl, Accessory Gland (a) Fluid; Spz, Spermatozoa; Vd, Vas deferens; X, Unknown structure; XFI, Fluid of unknown structure.

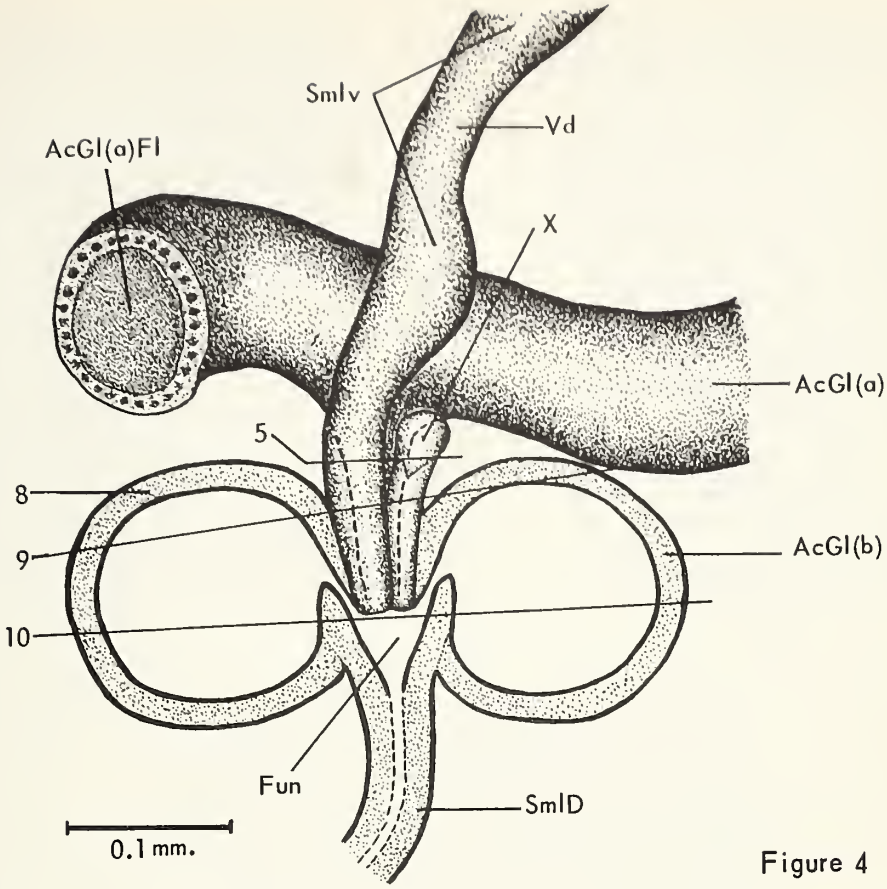


Figure 4

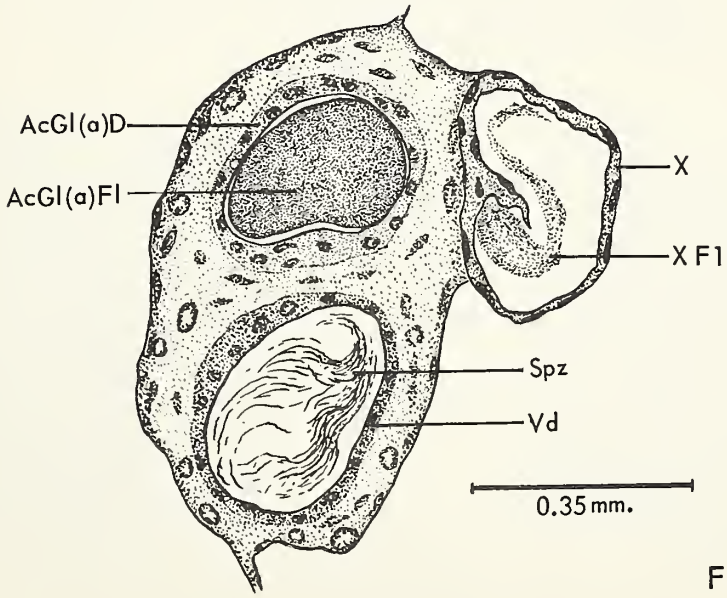


Figure 5

PLATE 5

Fig. 6. Enlarged view of a section through the testis follicle showing the various nuclei; Delafield's hematoxylin with eosin. Sep, Septum; Spz, Spermatozoa. X300.

Fig. 7. Similar view of the testis follicle as in fig 6, showing nuclei of different sizes; Delafield's hematoxylin with eosin. EpSh, Epithelial Sheath; Spz, Spermatozoa. X300.

Fig. 8. Longtitudinal section through AcGl(b) showing the gland structure and funnel portion; Delafield's hematoxyli with eosin. AcGl(b), Accessory Gland (b); Fun, Funnel; Nuc, Nucleus. X300.

Fig. 9. Transverse section through AcGl(b) showing the central tri-duct system which leads into the funnel; Delafield's hematoxylin with eosin. AcGl(a)D, Accessory Gland (a) Duct; AcGl(b), Accessory Gland (b); Vd, Vas deferens X, Unknown structure. X130.

Fig. 10. Transverse section through AcGl(b), but slightly posterior to the section in fig. 9. The large single median duct is the funnel filled with fluid of the accessory glands and spermatozoa; Delafield's hematoxylin with eosin. AcGl(b), Accessory Gland (b); Fun, Funnel. X130.

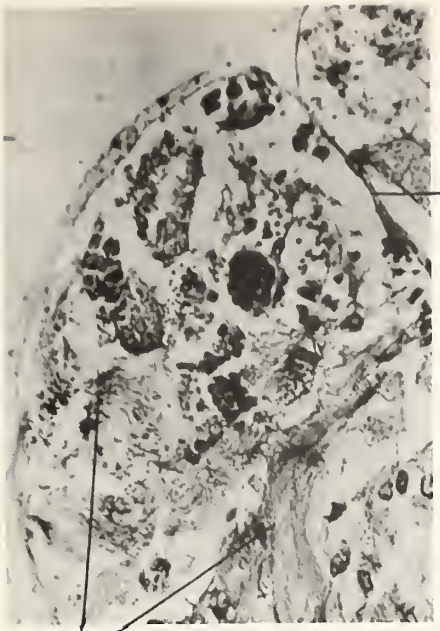


Figure 6

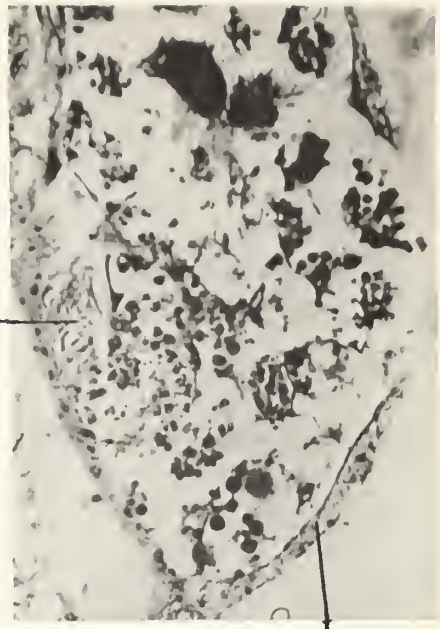


Figure 7

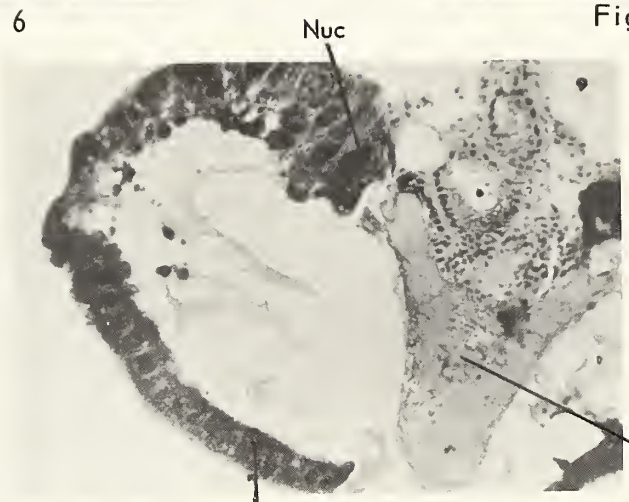


Figure 8

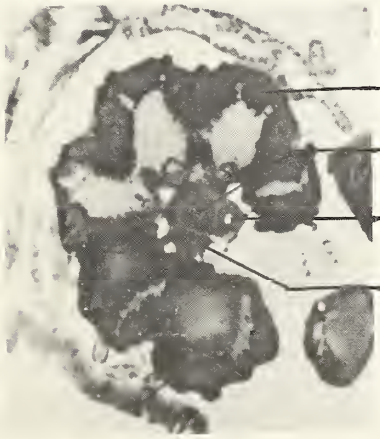


Figure 9

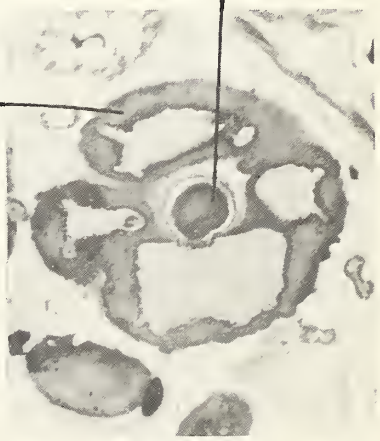


Figure 10

PLATE 6

Fig. 11A, B, C, D, and E. Drawings of the male copulatory organ in various aspects. Figs. A, B, and C specifically show all sclerotized parts while figs. D and E illustrate most of the musculature. All structures are illustrated in the normal resting position. Anch, Anchor; Apex; Apod, Apodeme; BOr, Basal Orifice; LPen, Lateral fold of Penis; M_1 - M_{11} inclusive, specific muscles; Ost, Ostium; Pen, Penis; SensPen, Sensory spines on Penis; SmlRd, Seminal Rod; Spcl, Spicule; Teg, Tegmen.

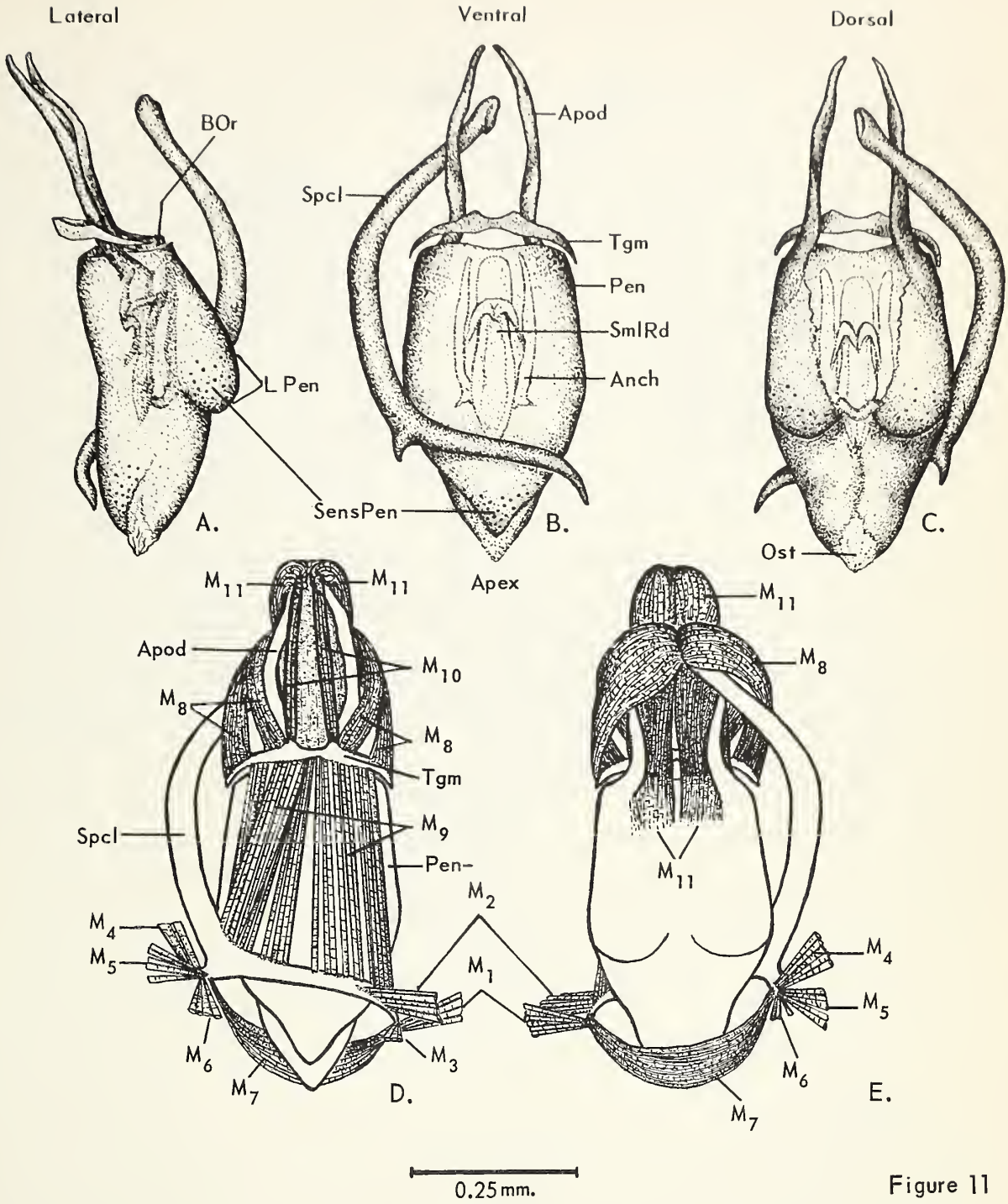

Lateral
Ventral
Dorsal
BOr
L Pen
SensPen
A.
Apod
Spcl
Tgm
Pen
SmlRd
Anch
B.
C.
Ost
Apex
M_{11}
M_{11}
Apod
M_{10}
M_8
M_8
Tgm
Spcl
M_9
Pen
M_2
M_1
M_4
M_5
M_6
M_7
M_3
D.
M_{11}
M_8
M_{11}
M_4
M_5
M_6
M_7
E.
0.25 mm.

Figure 11

PLATE 7

Fig. 12A and B. Longtitudinal ventral view of the posterior male abdomen showing the musculature and accessory sclerites of the copulatory organ when in the mating position. Note penis external to the abdomen, spicule remains stationary, the tegmen is pulled to a posterior position, M_8 is fully expanded, and M_9 fully contracted. Fig. B is an enlarged cross sectional view of the ejaculatory duct. Apod, Apodeme; CMcl, Circular Muscle; $ConnMm^1$, first Connecting Membrane; EjD, Ejaculatory Duct; M_1, M_2, M_4, M_5, M_6, M_7, M_8, M_9, M_{11}, specific muscles; Pen, Penis; S, Sternum; SmlD, Seminal Duct; Spcl, Spicule; T, Tergum; Tgm, Tegmen.

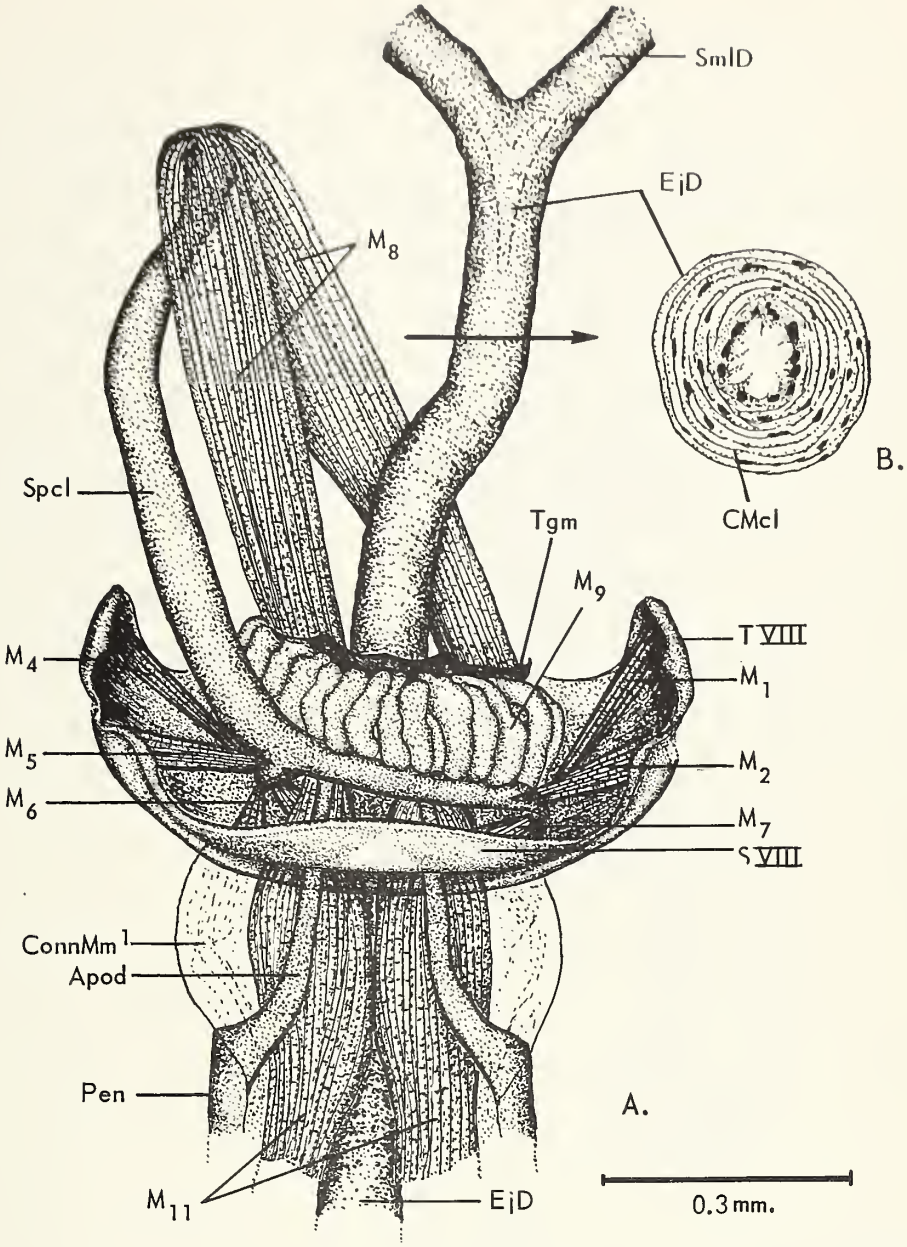

SmID
EjD
M8
B.
CMcl
Spcl
Tgm
M9
T VIII
M4
M1
M5
M2
M6
M7
S VIII
ConnMm1
Apod
Pen
A.
M11
EjD
0.3 mm.

Figure 12

PLATE 8

Fig. 13. Dorsal view of the male copulatory organ extended for the mating position. The internal sac is fully everted. Note the position of the gonopore, internal muscle attachments, and spiny armature of the membranous lobes of the internal sac. Apod, Apodeme; $ConnMm^1$, first Connecting Membrane; EjD, Ejaculatory Duct; Gpr, Gonopore; IntSa, Internal Sac; LLb, Lateral Lobe of internal sac; LPen, Lateral fold of Penis; M_{11}, M_{12}, internal muscles of penis; MLb, Median Lobe of internal sac; Pen, Penis; SmlRd, Seminal Rod; T, Tergum.

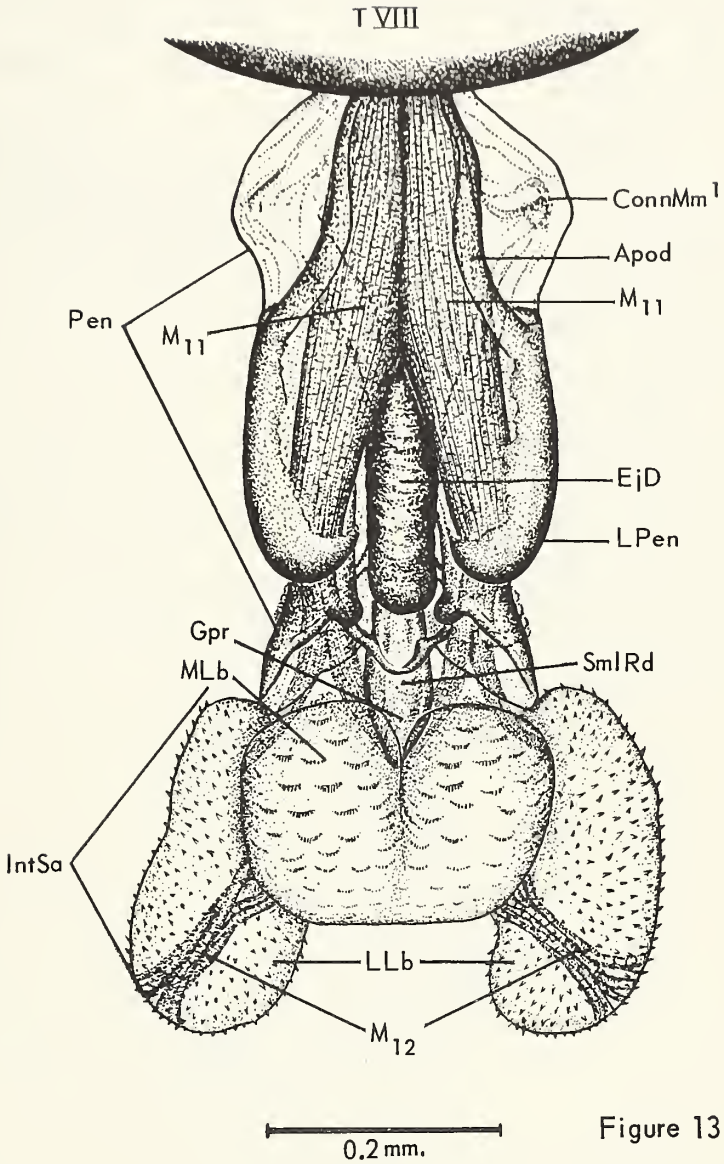

T VIII
ConnMm 1
Apod
M 11
Pen
M 11
EjD
LPen
Gpr
MLb
SmlRd
IntSa
LLb
M 12
0.2 mm.

Figure 13

PLATE 9

Fig. 14. Lateral view of the male copulatory organ external to the abdomen and with the internal sac fully everted. Note the terminal muscle attachments, the lack of spiny armature on the terminal and ventral side of the median lobe, position of the gonopore, and the Y-structure. The internal accessory apparatus is not outlined. Abd, Abdomen; Apod, Apodeme; $ConnMm^1$, first Connecting Membrane; Gpr, Gonopore; IntSa, Internal Sac; LLb, Lateral Lobe of internal sac; LPen, Lateral fold of Penis; M_{11}, M_{12}, internal muscles of penis; MLb, Median Lobe of internal sac; Pen, Penis; S, Sternum; T, Tergum; Y, Unknown structure of internal sac.

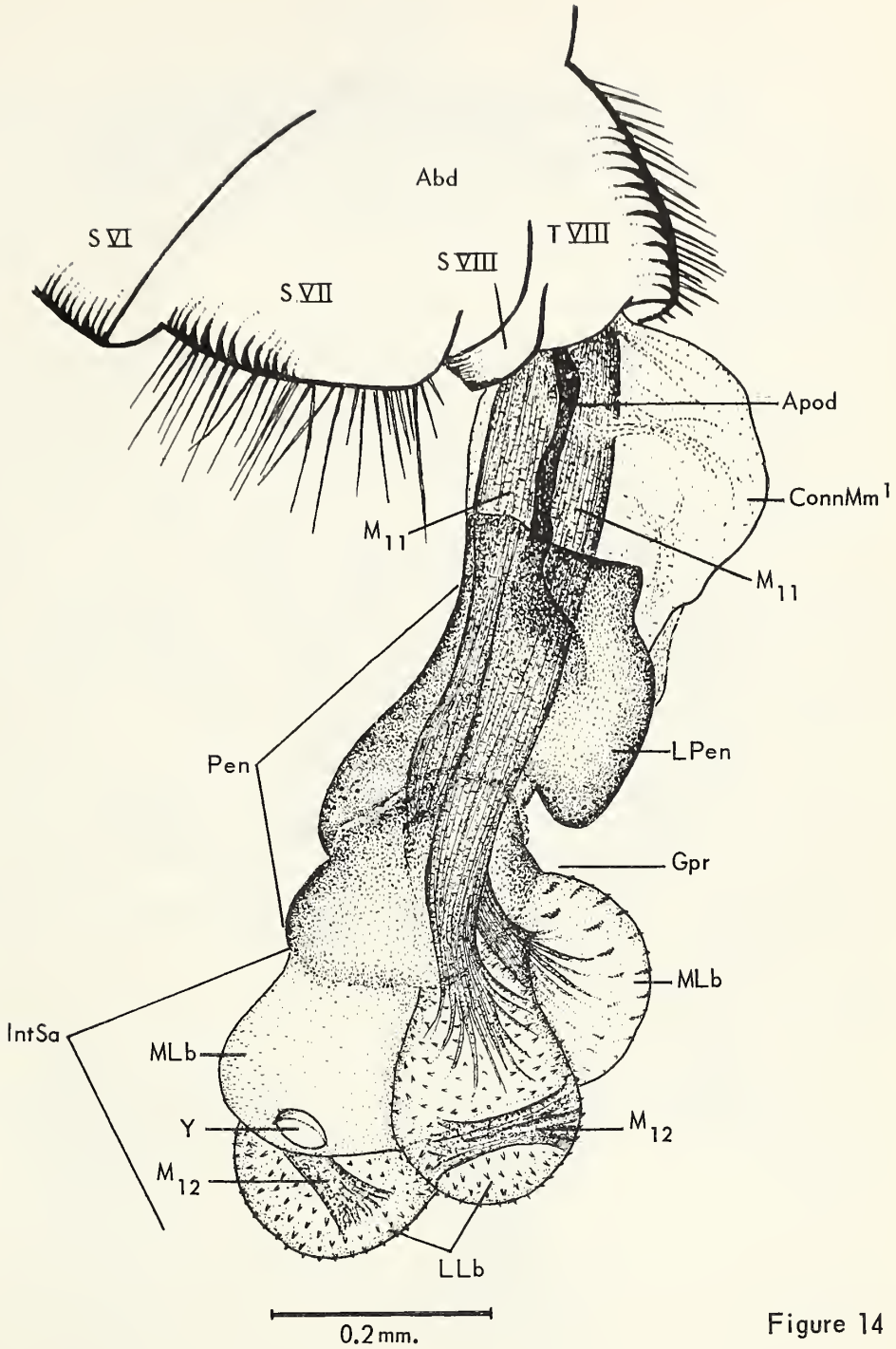

Abd
S VI
S VII
S VIII
T VIII
Apod
ConnMm 1
M 11
M 11
Pen
LPen
Gpr
MLb
IntSa
MLb
Y
M 12
M 12
LLb
0.2 mm.

Figure 14

[illegible]

[illegible]

PLATE 10

Fig. 15. Cross section through the Y-structure showing its position within the penis organ. Cut, Cuticle; IntSa, Internal Sac; Pen, Penis; Y, Unknown structure of internal sac.

Fig. 16. Transverse section through the penis organ at a near median plane, showing the ejaculatory duct attachment to the internal accessory apparatus and the gland substance composed primarily of AcGl(a)Fl. AcGl(a)Fl, Accessory Gland (a) Fluid; Arm, Arm of anchor; Cut, Cuticle; EjD, Ejaculatory Duct; IntSa, Internal Sac; SmlRd, Seminal Rod.

Fig. 17A and B. Ventral and lateral views of the internal accessory apparatus of the male genitalia. Anch, Anchor; Arm, Arm of anchor; Ejd, Ejactulatory Duct; Gpr, Gonopore; SmlRd, Seminal Rod.

Fig. 18. Top and side views of a sensory spine of the penis organ. Cut, Cuticle; SensPen, Sensory spine of Penis.

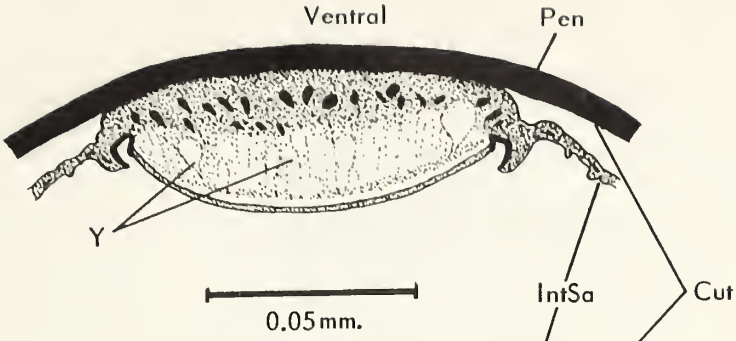


Figure 15

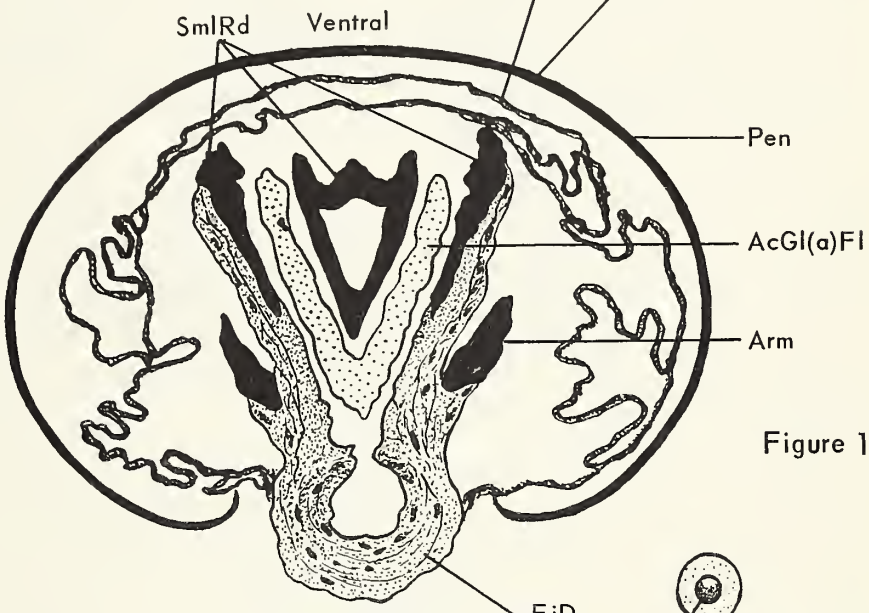


Figure 16

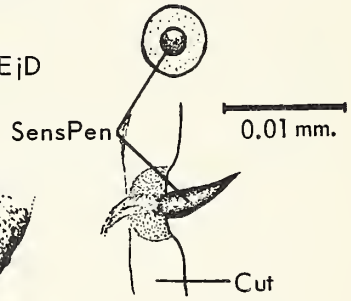


Figure 18

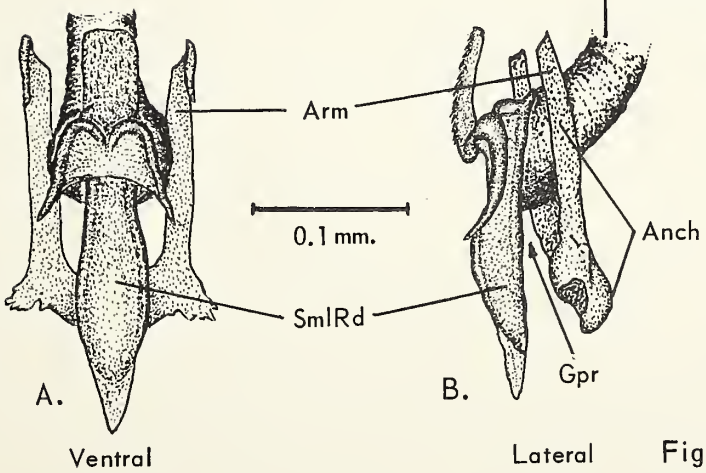


Figure 17

PLATE 11

Fig. 19. Ventral view of a newly developed female reproductive system with posterior attachments to the abdominal segments. Abd, Abdomen; AcGl, Accessory Gland; Anus; Clx, Calyx; Bcopx, Bursa copulatrix; GenOp, Genital Opening; LOvd, Lateral Oviduct; MOvd, Median Oviduct; Ov, Ovary; Ovl, Ovariole; S, Sternum; Spth, Spermatheca; SusLig, Suspensory Ligament; T, Tergum.

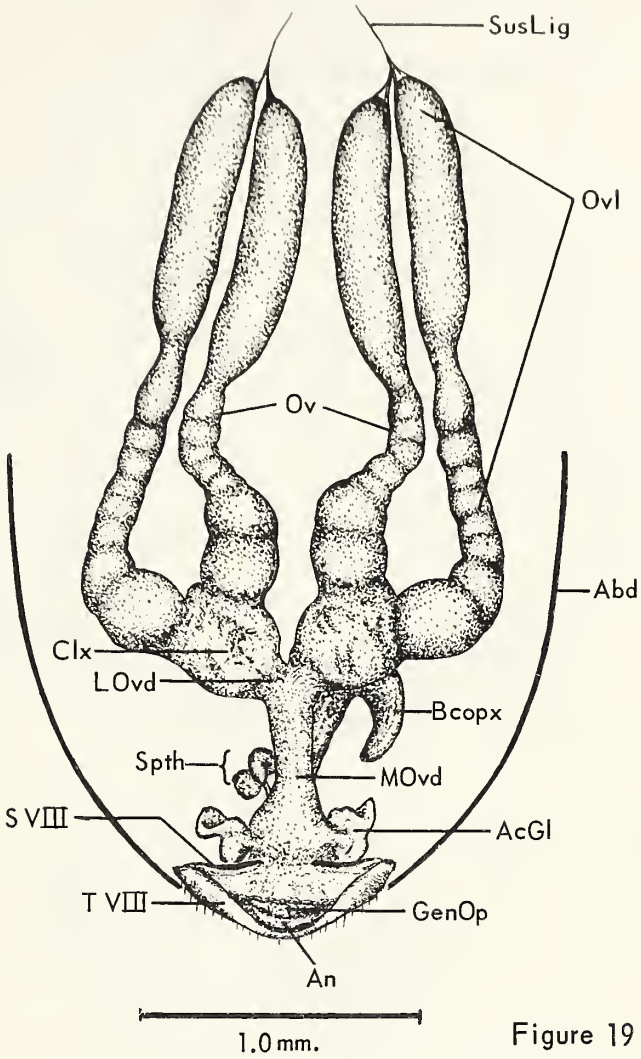
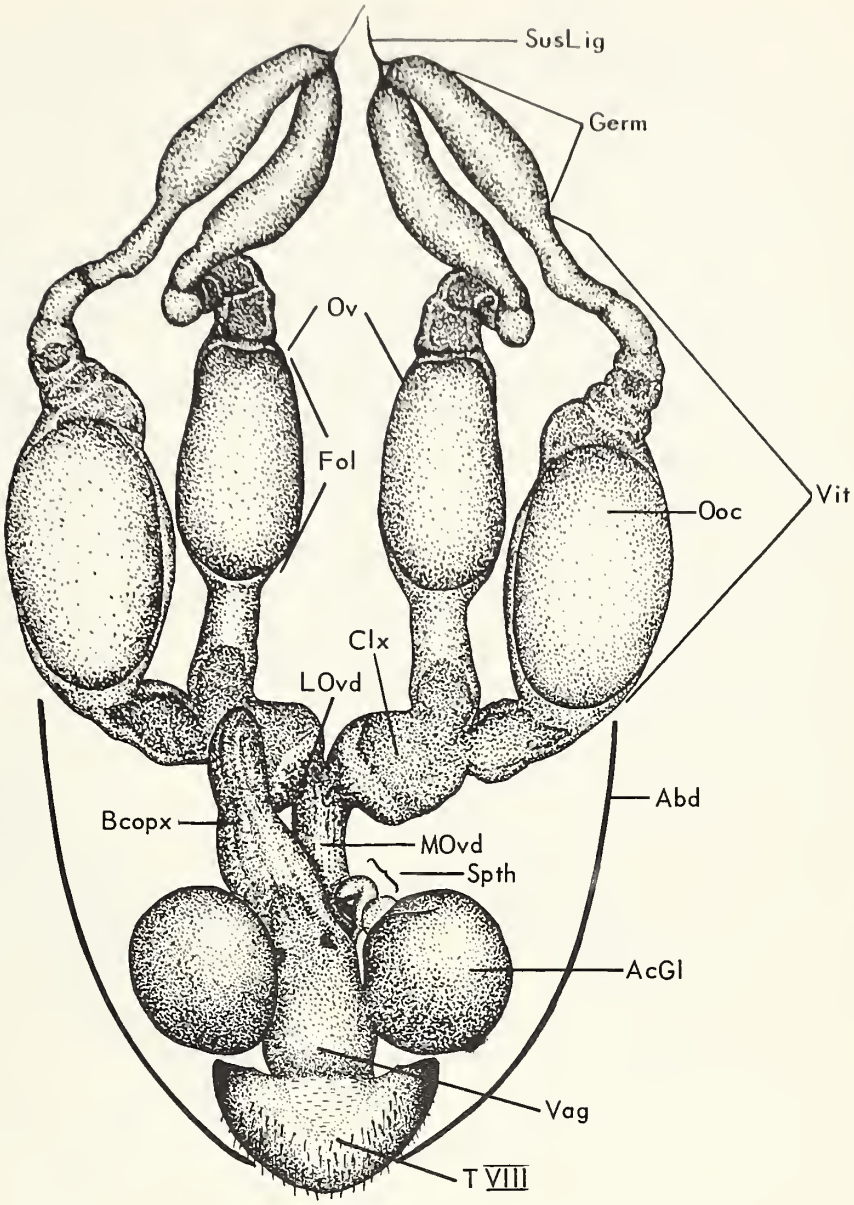

SusLig
Ovl
Ov
Abd
Clx
LOvd
Bcopx
Spth
MOvd
S VIII
AcGl
T VIII
GenOp
An
1.0 mm.

Figure 19

PLATE 12

Fig. 20. Dorsal view of a mature female reproductive system collected in the overwintering stage. Note nearly mature oocytes in the vitellarium, accessory glands filled to capacity, and the bursa copulatrix is turgid. A substance which is likely yolk material is present in the vagina and calyx regions. Abd, Abdomen; AcGl, Accessory Gland; Clx, Calyx; Bcopx, Bursa copulatrix; Fol, Follicle; Germ, Germarium; LOvd, Lateral Oviduct; MOvd, Median Oviduct; Ooc, Oocyte; Ov, Ovary; Spth, Spermatheca; SusLig, Suspensory Ligament; T, Tergum; Vag, Vagina; Vit, Vitellarium.



1.0 mm.

Figure 20

PLATE 13

Fig. 21A and B. Lateral view of the abdomen in a near median plane, showing the posterior attachment of the female reproductive system. Note the thickened musculature at the posterior end of the median oviduct and vagina and the opening of the spermathecal duct. The genital opening is continuous with the vagina and the median oviduct. Fig. B is an enlargement of the external sensory spines. Anus; Bcopx, Bursa copulatrix; Cut, Cuticle; GenOp, Genital Opening; Lum, Lumin; Mcl, Muscle; MOvd, Median Oviduct; Rec, Rectum; S, Sternum; SensAbd, Sensory spines on Abdomen; SpthD, Spermathecal Duct; T, Tergum; Vag, Vagina.

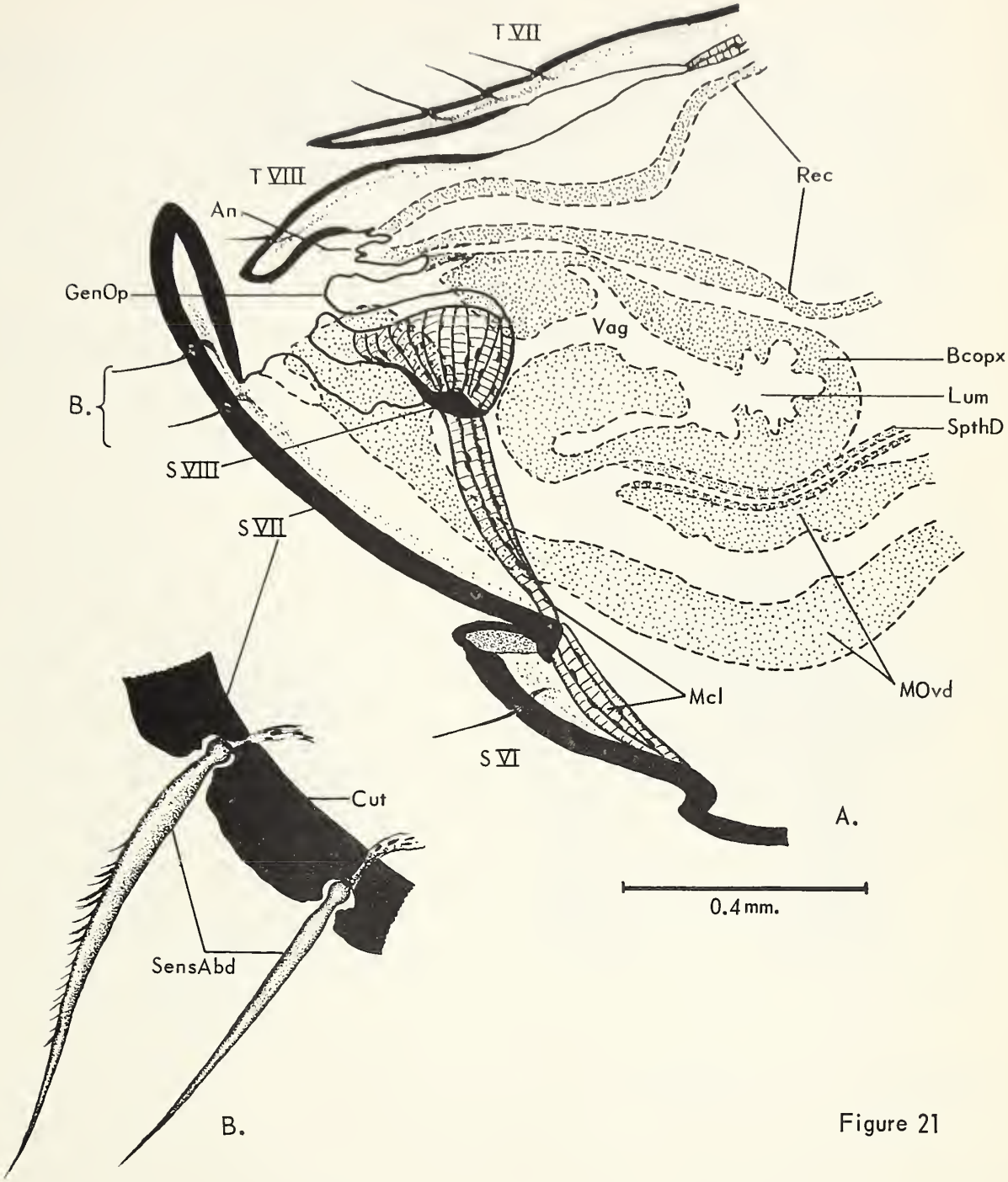

T VII
T VIII
An
Rec
GenOp
Vag
Bcopx
B.
Lum
SpthD
S VIII
S VII
MOvd
McI
S VI
Cut
A.
0.4 mm.
SensAbd
B.

Figure 21

PLATE 14

Fig. 22A and B. Dorsal view of the bursa copulatrix and associated structures. Note the assymmetry of the bursa copulatrix and spermatheca, and the constriction and spiny sclerites at the base of the bursa. Fig. B is an enlarged lateral view of the spiny sclerite. AcGl, Accessory Gland; Bcopx, Bursa copulatrix; Clx, Calyx; LOvd, Lateral Oviduct; MOvd, Median Oviduct; Scl, Sclerite of bursa copulatrix; Spth, Spermatheca; Vag, Vagina.

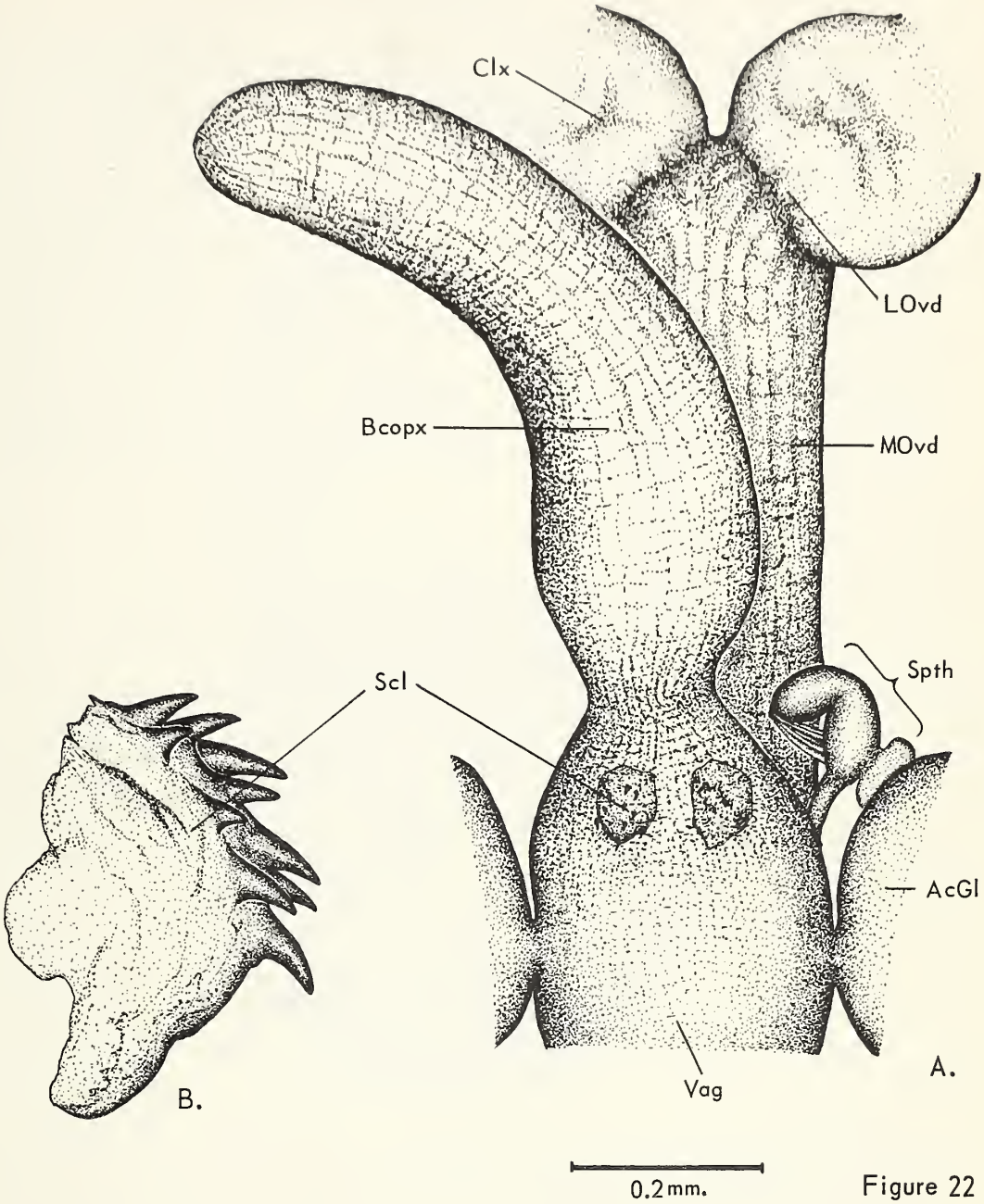
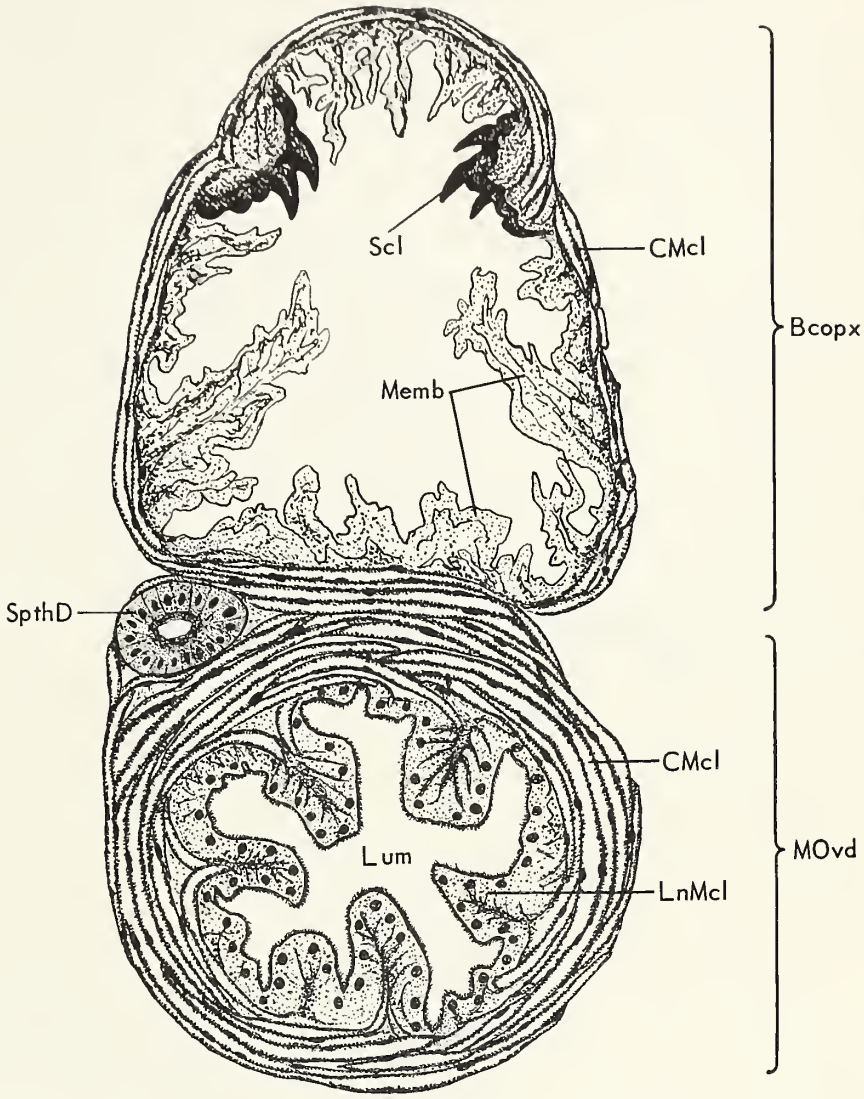


Figure 22

PLATE 15

Fig. 23. Transverse section of the median oviduct, bursa copulatrix, and spermathecal duct. Note the muscular arrangement, convolutions of the median oviduct, and membrane and sclerites of the bursa copulatrix. Bcopx, Bursa copulatrix; CMcl, Circular Muscle; LnMcl, Longtitudinal Muscle; Lum, Lumin; Memb, Membrane; MOvd, Median Oviduct; Scl, Sclerite of bursa copulatrix; SpthD, Spermathecal Duct.



0.1 mm.

Figure 23

PLATE 16

Fig. 24A, B, and C. Diagramatic drawing through a transverse section of the posterior end of the female reproductive system with cellular details of the accessory glands. Note opening from the vagina into the accessory glands, also the median ventral groove of the vagina, and the spermathecal duct. Fig. B represents an external view of the accessory gland cell. Fig. C illustrates the cell profile with its spined tip. AcGl, Accessory Gland; AcGlCl, Accessory Gland Cell; Bcopx, Bursa copulatrix; Mcl, Muscle; MOvd, Median Oviduct; Spn, Spines of accessory gland; SpthD, Spermathecal Duct; Vag, Vagina.

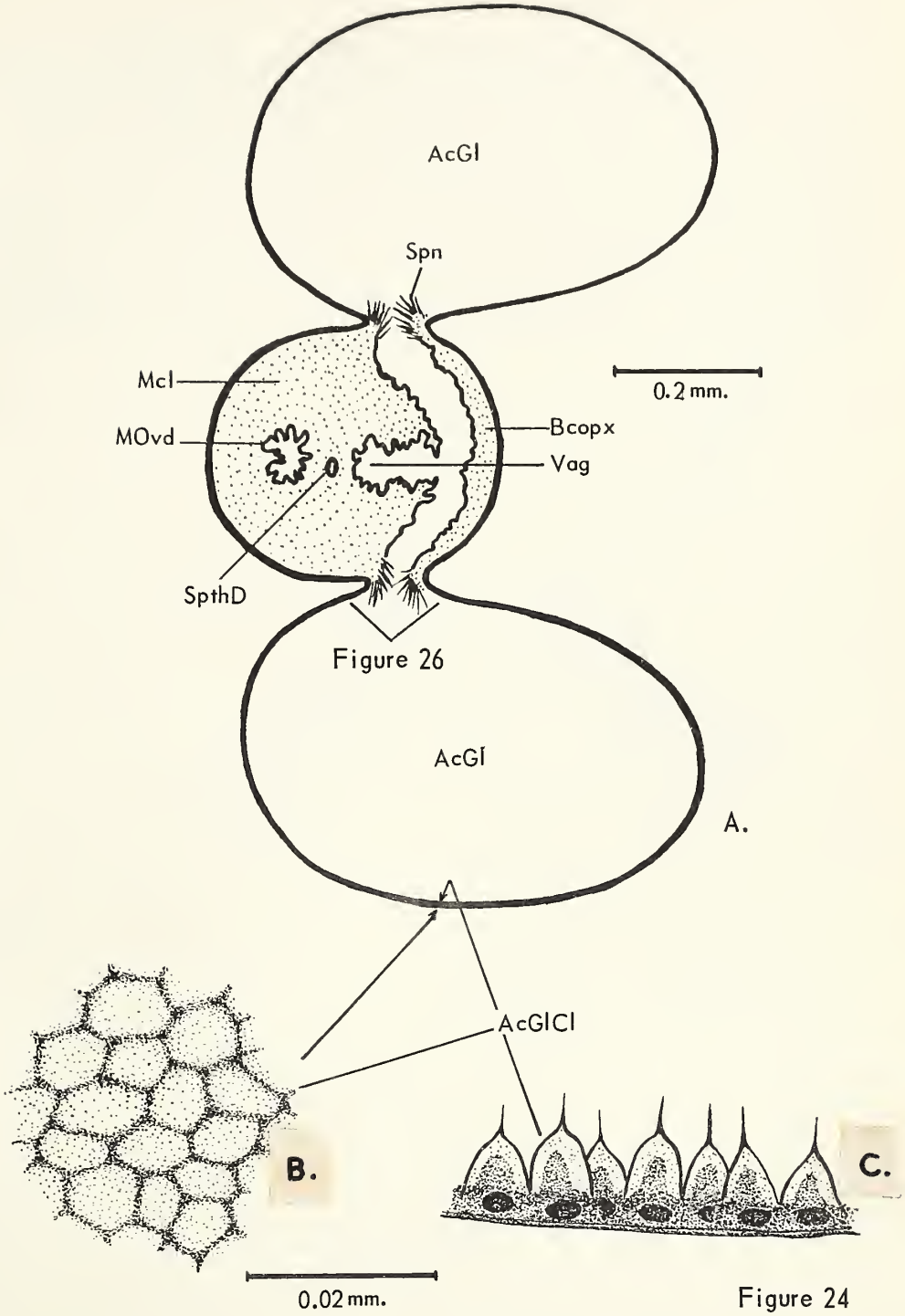

AcGl
Spn
Mcl
MOvd
Bcopx
Vag
SpthD
0.2 mm.
Figure 26
AcGl
A.
AcGlCl
B.
C.
0.02 mm.

Figure 24

PLATE 17

Fig. 25. Section through the opening of an accessory gland. Note the muscle arrangement, spines around the opening, and the gland cells. AcGl, Accessory Gland; AcGlCl, Accessory Gland Cell; Bcopx, Bursa copulatrix; CMcl, Circular Muscle; Memb, Membrane; Spn, Spine of the accessory gland.

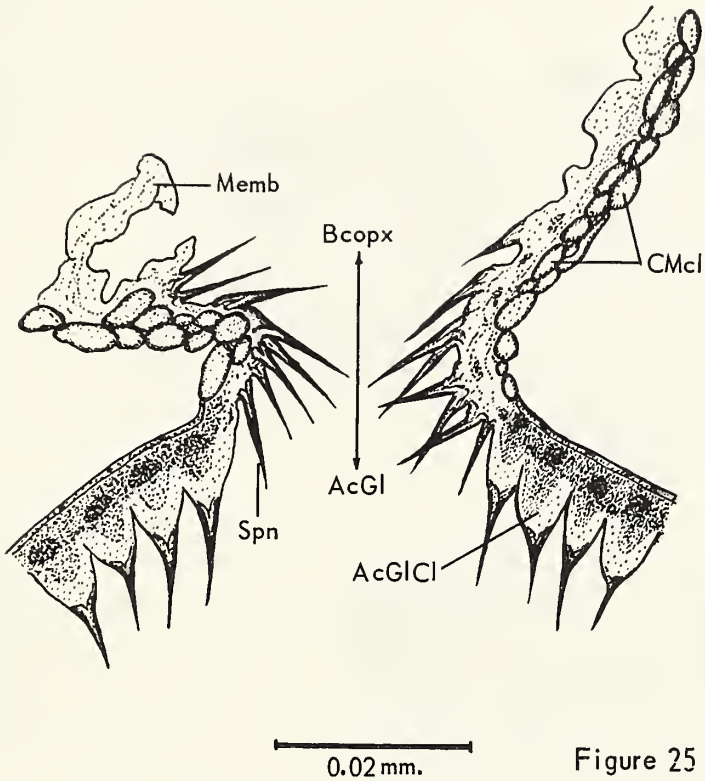


Figure 25

PLATE 18

Fig. 26. Diagramatic representation of an ovariole at maximum egg development, showing the major zones. Fol, Follicle; Germ, Germarium; Ooc, Oocyte; TlFil, Terminal Filament; Vit, Vitellarium.

Fig. 27. Enlarged view of the anterior tip of an ovariole from an egg laying female, showing large nuclei; Delafield's hematoxylin with eosin. Nuc, Nucleus; TlFil, Terminal Filament. X 300.

Fig. 28. Enlarged longtitudinal section through a median region of the germarium of a newly developed female. Note the two sizes of muclei, the largest are the most numerous; Delafield's hematoxylin with eosin. Nuc, Nucleus. X 300.

Fig. 29. Enlarged longtitudinal section taken from the same region of the germarium as in fig. 28, except that it is from an egg laying female. Note the size of nuclei in comparison with the nuclei in fig. 28; Delafield's hematoxylin with eosin. Nuc, Nucleus. X 300.

Fig. 30. Enlarged longtitudinal section showing the transition zone where the young oocytes are differentiated and the lateral stratification of the prefollicular epithelial cells. This ovariole was taken from an egg laying female; Heidenhain's hematoxylin with eosin. EpSh, Epithelial Sheath; Ooc, Oocyte; PrefolEpth, Prefollicular Epithelium. X 300.

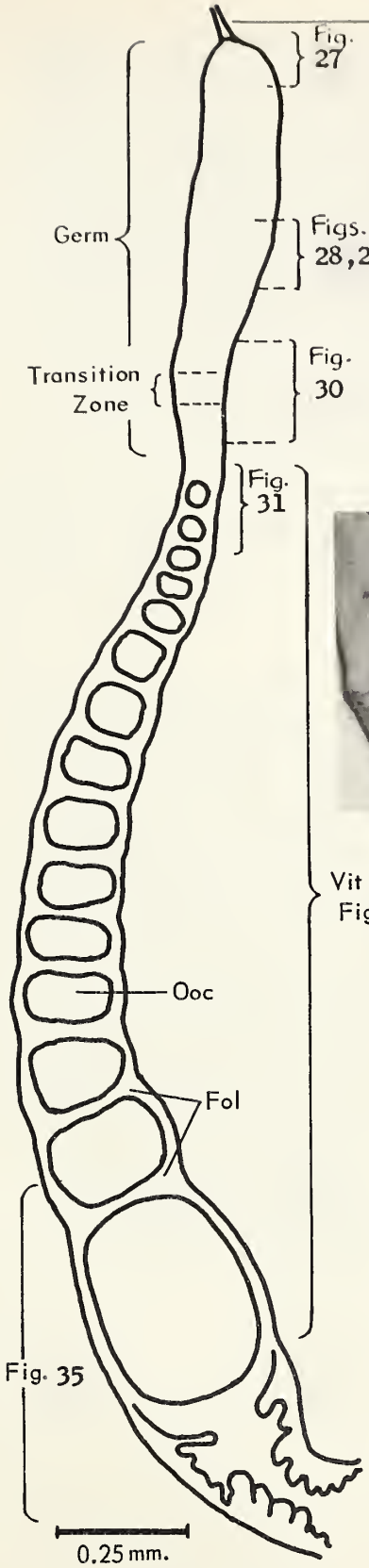


Figure 26

Figure 27

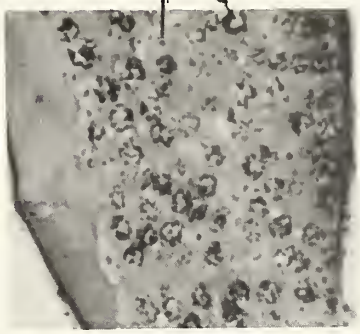


Figure 28

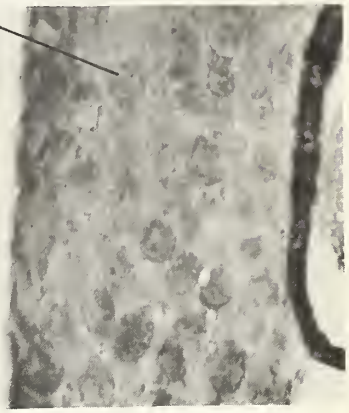


Figure 29

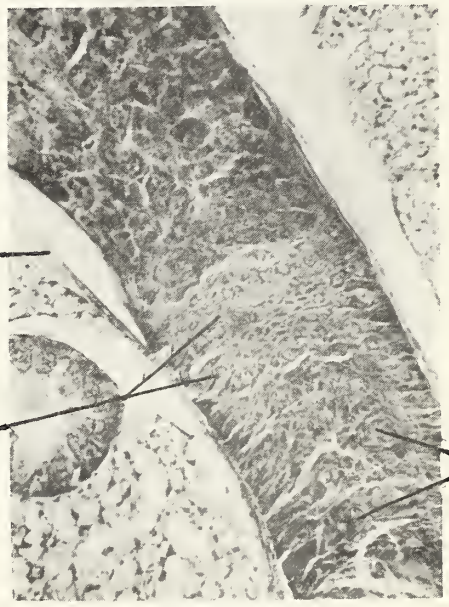


Figure 30

Nuc

PLATE 19

Fig. 31. This section is a continuation of fig. 30 and shows the immature oocytes embedded in prefollicular epithelial cells; Heidenhain's hematoxylin with eosin. EgNuc, Egg Nucleus; EpSh, Epithelial Sheath; Ooc, Oocyte; PrefolEpth, Prefollicular Eputhelium. X 300.

Fig. 32. Section through an ovariole at maximum egg production, showing the characteristic compact configuration. The germarium portion is missing. Note the yolk spherules forming in the three largest oocytes; Delafield's hematoxylin with eosin. EgNuc, Egg Nucleus; FolEpth, Follicular Epithelium; Ooc, Oocyte. X 80.

Fig. 33. Section through the spermathecal gland and pump organ, showing the histological structure of the sac. Note also the valve like opening and the spermatozoa in both structures; Delafield's hematoxylin with eosin. SpthPm, Spermathecal Pump; SpthSa, Spermathecal Sac; SpthVI, Spermathecal Valve; Spz, Spermatozoa. X 300.

Fig.34. Section through the spermatheca to specifically show the valve like opening. Heidenhain's hematoxylin with eosin. CmpMcl, Compressor Muscle; SpthPm, Spermathecal Pump; SpthSa, Spermathecal Sac; SpthVI, Spermathecal Valve; Spz, Spermatozoa. X 300.

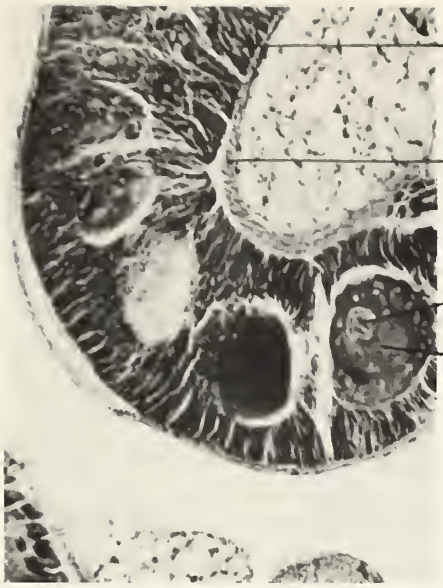


Figure 31

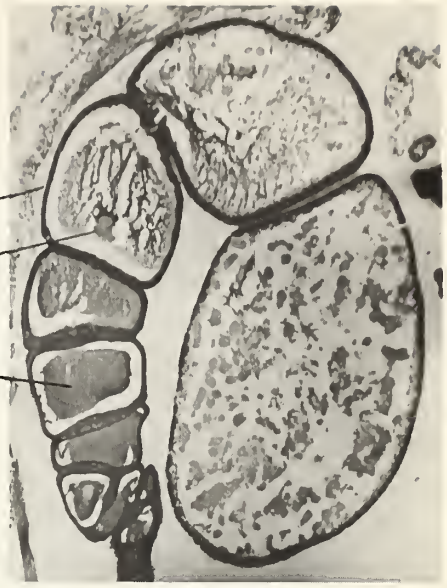


Figure 32

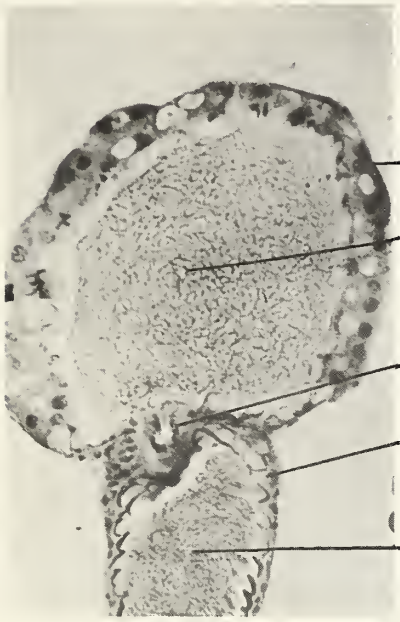
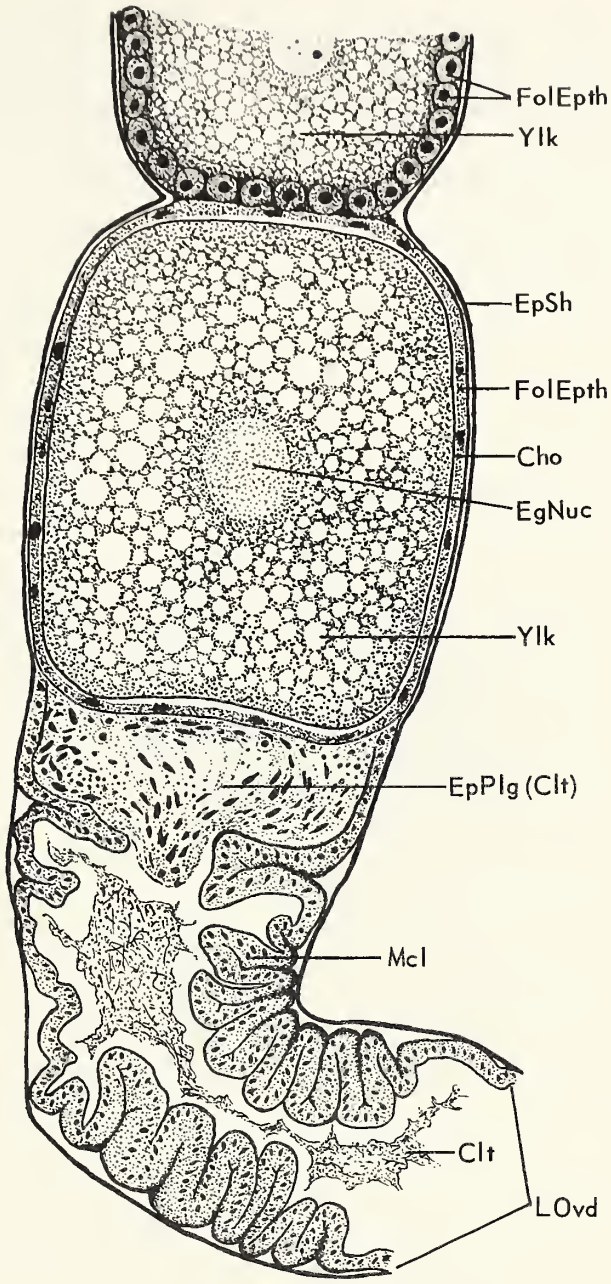


Figure 33

Figure 34

PLATE 20

Fig. 35. Longtitudinal view of the basal vitellarium showing a mature oocyte, epithelial plug (corpus luteum), and the muscular calyx region. Note also the uninucleate follicular cells. The egg nucleus in this case is probably analogous with the germinal vesicle described for other insects. Cho, Chorion; Clt, Corpus luteum; EgNuc, Egg Nucleus; EpPlg, Epithelial Plug; EpSh, Epithelial Sheath; FolEpth, Follicular Epithelium; LOvd, Lateral Oviduct; Mcl, Muscle; Ylk, Yolk.



0.3 mm.

Figure 35

PLATE 21

Fig. 36. External side view of a spermatheca, showing all parts. Note the sculptured pattern. CmpMcl, Compressor Muscle; SpthD, Spermathecal Duct; SpthPm, Spermathecal Pump; SpthSa, Spermathecal Sac.

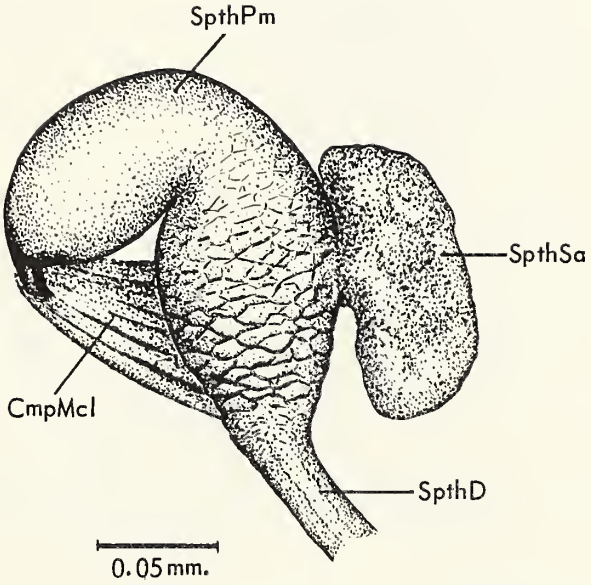


Figure 36

PLATE 22

Fig. 37. Section through the entire spermatheca. Note the orientation of the spermatozoa in the pump organ, the outer epithelial sheath, and the internal sculpture. CmpMcl, Compressor Muscle; EpSh, Epithelial Sheath; SpthD, Spermathecal Duct; SpthPm, Spermathecal Pump; SpthSa, Spermathecal Sac; SpthVl, Spermathecal Valve; Spz, Spermatozoa.

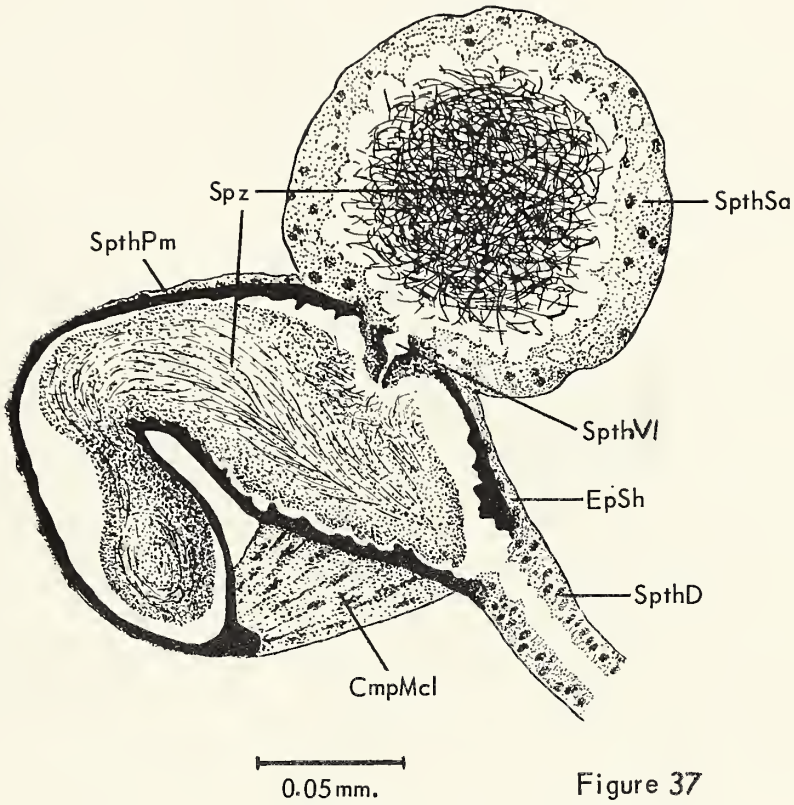


Figure 37